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## OCTOCORALS

## PART I. PENNATULARIANS

*by*

Hjalmar Broch

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## PART I. PENNATULARIANS

By

HJALMAR BROCH

The Zoological Laboratory, Oslo-Blindern, Norway

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# OCTOCORALS

## PART I. PENNATULARIANS

By Hjalmar Broch

(The Zoological Laboratory, Oslo-Blindern, Norway)

(Plates XI and XII, text-figures 1–5)

## INTRODUCTION

THE Discovery collections of pennatularians are not very extensive. This is not especially surprising, because the structure of the species living at greater depths and their mode of life on the muddy bottom enable them to escape most collecting gear, a fact emphasized on an earlier occasion (Broch 1957).

The collections include the following species:

*Cavernularia elegans* (Herklots)
*Veretillum cynomorium* (Pallas)
*Actinoptilum molle* Kükenthal
*Renilla mülleri* Kölliker
*Umbellula lindahli* Kölliker
*Pennatula rubra* Ellis
*Pteroëides griseum* (Bohadsch)

With the exception of *Umbellula lindahli*, all the species belong to the coastal shelf waters and mostly to shallow depths above some 100 m. *Renilla mülleri* is an American species, whereas the others belong to the Atlanto-African fauna, *Actinoptilum molle* being known only from the coastal waters of South Africa.

The genus *Umbellula* was represented by comparatively rich material from Antarctic waters, and I therefore seized the opportunity to make a critical study of the much disputed species of this genus. An introduction to such a revision has recently been published in the report on the pennatularians of the Swedish Deep-Sea Expedition (Broch 1957). A broader survey on the other hand, necessitated both material from different areas as well as a re-examination of types described from earlier expeditions: especially those from the 'Challenger' Expedition. This work was made possible by a grant from the National Institute of Oceanography; I am greatly indebted to Dr N. A. Mackintosh who arranged this for me, thus allowing me to extend the scope of my study beyond the strict limits of the Discovery collections.

Prior to 1939, Mrs L. M. I. MacFadyen (neé Dean) worked on these collections at the British Museum, but for various reasons she was unable to write an account. After the war the whole collection was sent to me for report, together with her valuable notes. By agreement with Mrs MacFadyen I have made full use of these notes as indicated in the text.

My work at the British Museum (Natural History) was facilitated in every way by Miss Helene E. Bargmann of the staff of the National Institute of Oceanography, and by Dr W. J. Rees and Mr Ernest White of the Museum. I wish to express my gratitude for their never-ceasing aid and counsel on all occasions.

## VERETILLIDAE

### Some general remarks on the family

Hickson (1916) emended the definition of this family to include the genus *Actinoptilum*, which Kükenthal and Broch (1911) had united with *Echinoptilum* in the family Echinoptilidae, the zooids having more or less distinctly developed calices. Hickson maintained that the 'calices' mentioned by Kükenthal and Broch in *Actinoptilum* were verrucae not calices. It is not clear, where we ought to draw the line between a calix and a verruca; in *Actinoptilum* these structures are quite rudimentary and consist only of two rather small, low teeth. Two corresponding teeth have been developed in *Echinoptilum*; indeed in *E. echinatum* they are remarkably large, and in this species Hickson did acknowledge them to be part of a calix. But it is impossible to tell whether the smaller teeth of *Actinoptilum* are a commencement (oriment) or the remnants (rudiments) of a calix or a verruca.

Much more stress must be laid on the external symmetry. Hickson quite correctly pointed out that the external features of *Actinoptilum* show no hint of bilateral symmetry and that accordingly the right place for the genus was among the Veretillidae. He also maintained that the Veretillidae are 'sea-pens in which the autozooids and siphonozooids are distributed without any definite arrangement in horizontal or longitudinal rows'. This statement, however, cannot be accepted. Both in *Veretillum* and in *Actinoptilum* longitudinal furrows divide the surface of the rachis into obvious longitudinal ribbon-like fields, each of which generally shows a single row of autozooids placed at somewhat varying intervals, so that they do not form regular transverse rows. Drawings of living specimens of *Veretillum cynomorium* (Kükenthal and Broch 1911, pl. XIII, fig. 1) show that in this species the siphonozooids form a single longitudinal row in the middle of the ribbon-like field, whereas in *Actinoptilum molle* they are irregularly placed, crowded on the 'ribbon', and generally arranged side by side.

Hickson (1916) agreed with Kükenthal and Broch (1911) that the Veretillidae probably stand near the ancestral sea-pens. After examination of specimens from the 'John Murray Expedition' and comparison with specimens from other collections, Hickson (1937) wrote: 'The consideration of these specimens confirms the view that I ventured to put forward in 1918 (p. 131) that in these radially symmetrical Veretillidae we have the most primitive forms of the Pennatulacea.' However, it is not clear, whether in this case he was referring to the genus *Cavernularia*, or the Veretillidae as a whole.

It is impossible to tell which form of spicules is the most primitive. But it is obvious that the spicules of the radially symmetrical Veretillidae in general are much more variable than those of the externally bilateral sea-pens. The development of the spicules has not yet been determined in the Veretillidae; nevertheless, there is much to be said for regarding the flat biscuit-shaped spicules as the most primitive. They occur in *Veretillum* and *Actinoptilum*, where an axis is wanting, as well as in the axiferous genus *Lituaria*. In *Actinoptilum*, however, the biscuit-shaped spicules are restricted to the stalk, whereas the rachis has three-flanged, rod- or needle-shaped spicules similar to the dominant type in the bilaterally symmetrical groups. The genus *Cavernularia*, in the wide sense of Hickson (1937), on the other hand, displays a great variation both in form and disposition of the spicules. In some species they are restricted to the surface layer, in others they also occur in great numbers in the inner tissues of the stalk. The spicules may be of uniform shape throughout, or they may have one shape in the surface tissues and another in the interior of the specimen. In one species the spicules are knobbed or branched at their ends, in others oval, slender spindles or needle-shaped. A revision of this genus is indeed needed, but must be based on extensive investigation of the variations and behaviour in living specimens.

*Cavernularia elegans* (Herklots 1858)

(Synonymy before 1910, see Kükenthal and Broch 1911.)
*Cavernularia elegans* + *C. madeirensis* + *C. pusilla*, Kükenthal 1915, pp. 15–17, figs. 19, 20.

St. 274. Off Angola, W. Africa, 65 m. 1 specimen (identified by Mrs MacFadyen).

In a note Mrs MacFadyen gives the following data concerning the specimen: 'A small club-shaped colony very similar in appearance to Kükenthal and Broch's photograph (1911, Pl. 18, fig. 29) shows

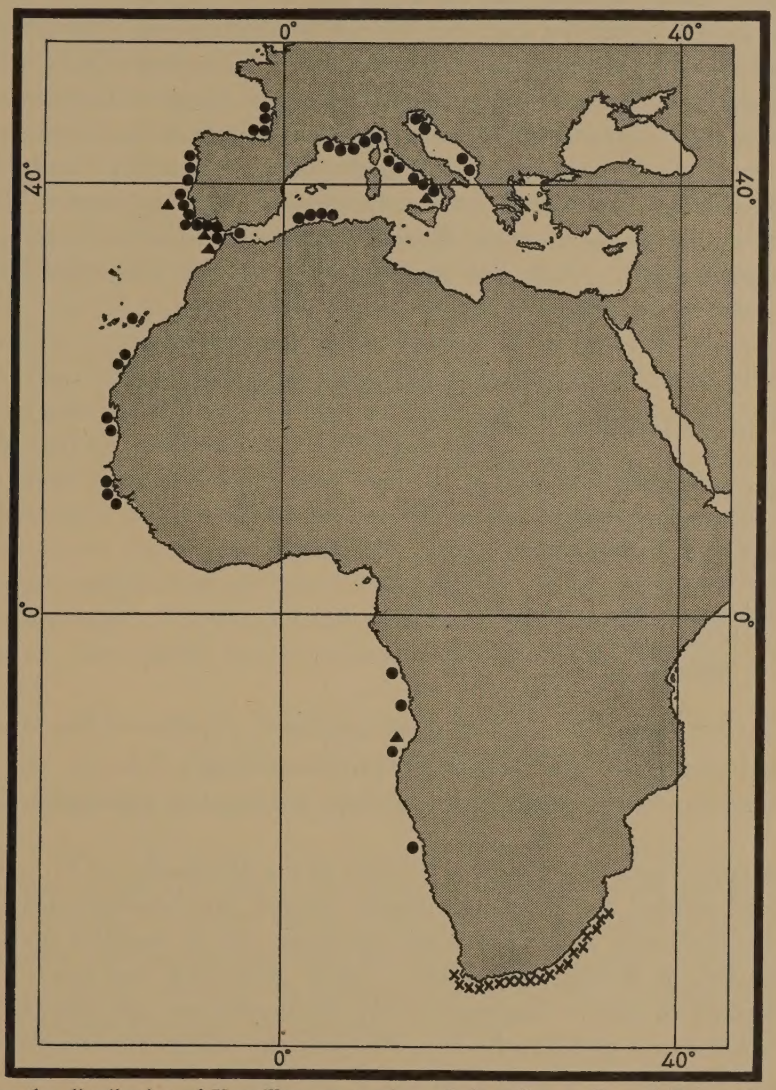


Fig. 1. Chart showing the distribution of *Veretillum cynomorium*, *Actinoptilum molle*, and *Pennatula rubra*. ● *Veretillum cynomorium* (mainly after Pax and Müller, 1954). × *Actinoptilum molle*. ▲ *Pennatula rubra*.

a head [rachis] 2·3 cm. long and 1·2 cm. broad and a stalk, 2·7 cm. long and 4 mm. broad at the top, 7 mm. broad near the base. The autozooids are up to 4 mm. long (excluding the tentacles) and 3 mm. in diameter. The siphonozooids are numerous, scattered between the autozooids on the head. There is no axis. The spicules are of the usual needle-like *Cavernularia* type. Small groups of minute almost rounded spicules ['calcareous concretions' Broch 1957] are formed in the inside of the stalk, a point

in which the species differs from *C. obesa* (also without an axis) which has larger and more numerous spicules inside the stalk.

'The colour of the colony is creamy with a dark brownish ring on the polyp just below where the tentacles arise.'

The species has been recorded both from the Indian Ocean and Japan, but Kükenthal (1915) queried these localities. Evidently these records need confirmation. The habitat of *C. elegans* almost coincides with that of *Veretillum cynomorium* (text-fig. 1), but exact positions along the West African coast are remarkably scanty, although the species is said to be a shallow-water form. *Cavernularia madeirensis* Studer 1878 is certainly a synonym, and the Mediterranean *C. pusilla* (Philippi 1835) also is based on a small specimen of *C. elegans*. Consideration of Kükenthal's (1915) definitions does not reveal any distinguishing characters of importance between all these three species.

It is correct to say that the Discovery specimen represents the first exact location of the species on the West African coast, all earlier statements being given in general terms. Studer (1878) was a little more precise in describing *C. madeirensis* from 90 m. depth on the west coast of Madeira, and Roule (1905) recorded the same species from the Atlantic Ocean near Morocco in 99 m. Kükenthal and Broch (1911) reported that *C. pusilla* was found at Palermo and Sicily, and Kölliker (1872) also queried a record from the Adriatic.

### *Veretillum cynomorium* (Pallas 1766)

(Synonymy before 1910, see Kükenthal and Broch 1911.)
*V. cynomorium* Kükenthal 1915, p. 12, figs. 12, 13.
*V. cynomorium* Stuart Thomson 1923, p. 59.
*V. cynomorium* J. A. Thomson 1927, p. 63.
*V. cynomorium* J. A. Thomson 1929, p. 10.
*V. cynomorium* Nobre 1931, p. 34.
*V. cynomorium* Broch 1953, p. 10.
*V. cynomorium* Pax & Müller 1954.
*V. cynomorium* Pax & Müller 1955, p. 90.

St. 272. Off Elephant Bay, Angola, W. Africa, 43–91 m. 2 specimens (identified by Mrs MacFadyen).

In a note Mrs MacFadyen writes: 'The larger has a total height of 8·5 cm. and a stalk of 1·7 cm. They are both quite typical specimens of this radially symmetrical Pennatulid. The colour is pale cream.'

Pax and Müller (1954) have recently given a review of the distribution of *V. cynomorium*, a species characteristic of the tropical and temperate eastern Atlantic and Mediterranean (text-fig. 1). The northern limit of its habitat is evidently the Bay of Biscay, and its southern border lies somewhere south of the great Bay of Whales, South Africa, where Kükenthal and Broch (1911) reported its occurrence. According to Stuart Thomson (1923) the species has not been found on the South African coast south and east of Saldanha Bay. Probably the colder currents check its advance just south of the Bay of Whales.

The species is limited to the shallower shelf-waters above some 100 m. If the identification of the specimen from 540 m. depth near the Canaries (28° 47′ N, 13° 44′ 45″ W, J. A. Thomson 1927) is proved to be correct, this occurrence probably depends on an erratic specimen which has managed to grow up and continue to live, in spite of having sunk to the bottom far below its normal habitat. Similar cases have been observed in other benthic animals; it is necessary to regard them with caution and not immediately to deduce an extended normal habitat from these probably sporadic occurrences.

### *Actinoptilum molle* Kükenthal 1910

*Cavernularia obesa* + *C. elegans* Hickson 1900, Part I, p. 89, Pl. 3, A, B.
*Actinoptilon molle* Kükenthal 1910, p. 51.
*Actinoptilum molle* Kükenthal & Broch 1911, p. 201, Pl. 13, figs. 3, 4; Pl. 18, fig. 37.
*A. molle* Kükenthal 1915, p. 20, fig. 22.
*A. molle* J. Stuart Thomson 1915, p. 3, Pl. 1, figs. 3, 4.
*A. molle* Hickson 1916, p. 41.
*A. molle* J. Stuart Thomson 1923, p. 81.

St. 91. False Bay, South Africa, 35 m. 4 specimens (identified by Mrs MacFadyen).

In a note Mrs MacFadyen writes: 'The largest 20·5 cm. in length of which 6·5 cm. consist of the rachis. In our specimens the colour of the stalk is pale yellow, of the rachis very pale pink, the polyp-tentacles are pale yellow, the polyp anthocodiae with deep red spicules. The vertical lines in the rachis as figured by Kükenthal and Broch are clearly seen.'

In the British Museum 5 additional specimens were examined: (1) 'South Africa', J. Stuart Thomson (S. J. Hickson coll.); (2) Gilchrist coll., St. 145, 29° 40′ 30″ S, 31° 20′ 00″ E, 42 fm. 12 July 1920; (3) Gilchrist coll., St. 188, 29° 36′ 30″ S, 31° 16′ 30″ E, 33 fm. 12 August 1920 (2 specimens); (4) Gilchrist coll., St. 453, 33° 34′ 30″ S, 27° 09′ 05″ E, 40 fm. 1 September 1920.

Stuart Thomson (1915) pointed out that *Actinoptilum molle* 'is probably the most common Pennatulid in South African Seas'. Later on he (1923) emphasized 'that it occurs in the colder water of Table Bay as well as in the warmer of Algoa Bay and False Bay'. The depth of the habitat ranges from 35 m. (Discovery St. 91) and down to 183 m. ('Pieter Faure' 1902).

The remarkably restricted habitat of *A. molle* (text-fig. 1) is rather astonishing, especially when we consider Stuart Thomson's words which indicate considerable tolerance to changes in temperature; one might therefore expect the species to penetrate farther northwards from Table Bay along the western coast of South Africa, although east of False Bay and as far as the east coast of Natal it is found living in warmer water. A limiting factor must exist, but with the data available it cannot be determined at present. The species may be found to disappear where the cold Benguela Current impinges on the coast.

## RENILLIDAE

### *Renilla mülleri* Kölliker 1872

(A complete synonymy of this American species was given by E. Deichmann 1936.)

St. W.S. 742. Off the southern coast of Chile, 38° 22′ S, 73° 41′ W, 58–47 m. 5 specimens.

The specimens are large and of a light violet colour. Deichmann writes that the species is distributed over 'Gulf of Mexico, Venezuela, Brazil—coast of Chile, west coast of Central America'. It seems unknown, whether the distribution along the South American coast is continuous, or if a gap exists southwards from Brazil along the Patagonian coast round the southern Chilean coast to the locality at which the species was taken by 'William Scoresby'.

## UMBELLULIDAE

### Revision of the genus *Umbellula*

In a recent paper (1957) I have given some comments on the taxonomy of *Umbellula*, beginning with the remark that 'certainly too many species have been described within this genus'. Both Kükenthal and Broch (1911), Kükenthal (1915) and Hickson (1916) gave extensive reviews of the genus, but a thorough critical revision of the species is needed and can to a large extent only be achieved by examination of the type specimens kept in museums all over the world.

As emphasized in my paper (1957) I agree with Hickson (1916) that the *Umbellula* species fall into two main groups, viz. those with spicules, and those without. On the other hand, I cannot share Hickson's opinion that the shape of the axis (especially above the hold-fast), whether quadrangular or round in section, is only of subordinate value taxonomically. To a marked degree, this shape is correlated with calcification: round axes generally being rather poorly or almost uncalcified, whereas quadrangular axes are as a whole heavily encrusted with lime. This character is doubtless constant in and characteristic of a species. It is necessary to emphasize that we are speaking of the axis, and not of the stem or the stalk with its cover of soft tissues (cf. the remark about Marshall's description of *U. gracilis*, p. 255).

Before going into details concerning the species of *Umbellula* and their synonymy, the following key may clarify the important taxonomic characters:

## Key to the species of *Umbellula*

I. With spicules.

A. Axis round, only feebly encrusted with carbonate of lime and very flexible. Two kinds of spicules, large and small, all round in transverse section, feebly fusiform or rod-shaped, often the larger with somewhat knobbed ends, and sprinkled with granulations. *Umbellula durissima* Köll.

B. Axis quadrangular, rather rigid and strongly encrusted with carbonate of lime. Spicules rod- or needle-shaped with three longitudinal ridges or flanges, sprinkled all over with small spines or warts. *U. thomsonii* Köll.

II. Without spicules.

A. Axis round, almost devoid of lime, thin and extraordinarily flexible.

(1) Cluster with rather small autozooids concentrated in a pompon on the distal end of the rachis. *U. huxleyi* Köll.

(2) Clusters with large autozooids irregularly placed on a rather long rachis forming a tassel. *U. spicata* Kükenthal

B. Axis quadrangular, richly encrusted with carbonate of lime.

(1) Axis thin but rigid and rather brittle. Autozooids numerous and small, packed in a pompon on the short distal end of rachis. Specimens at most some 35 cm. high. *U. pellucida* Kükenthal

(2) Axis variable, but generally rather thick and flexible. Autozooids large, in colder waters generally very large and often very numerous in the tassels and not especially crowded. Full-grown specimens seldom as small as 40 cm. *U. lindahli* Köll.

(The arctic *U. encrinus* L. is more robust in its entire construction. Its axis is thicker than that of *U. lindahli* which does not seem to exceed 2 mm. in its thinnest part just below the polypiferous rachis. The autozooids are larger than those of *U. lindahli*. Possibly only an extreme form of this species, see p. 270.)

## Spiculate species of *Umbellula*

The rich collection of *Umbellula* from the Swedish Deep-Sea Expedition indicated that as yet only two species with spicules can be distinguished with certainty. These species are above all characterized by the shape and structure of their spicules and by the construction of the axis.

### *Umbellula durissima* Kölliker 1880

*U. durissima* Kölliker 1880, p. 16, Pl. 8, figs. 32, 33.
*U. durissima* + *U. dura* J. A. Thomson & W. D. Henderson 1906, pp. 92, 93, Pl. 8, fig. 9.
*U. durissima* + *U. dura* J. A. Thomson & J. Ritchie 1906, p. 859, Pl. 1, fig. 5.
*U. eloisa* Nutting 1912, p. 43, Pl. 6, figs. 3, 3*a*.
*U. durissima* + *U. dura* + *U. eloisa* Kükenthal 1915, p. 56.
*U. durissima* Hickson 1916, p. 126.
*U. durissima* Broch 1957, pp. 360, 363, text-fig. 7, Pl. 1, fig. 5.

This very characteristic species has dimorphic spicules: (1) Spicules up to 3 mm. long form a narrow band along the aboral side of the pinnulae adjoining the strong band of similar large spicules along the aboral side of the tentacle stem, a short way below its base on the anthocodia. (2) Small fusiform spicules crowded in the surface tissues of autozooids and rachis. All the spicules are round in section, they are never three-flanged. The axis is round in section and remarkably feebly calcified in contrast to the heavy armoured autozooids with their calcareous spicules.

(Holotype: British Museum (Nat. Hist.). Reg. No. 1881. 2. 11. 21.)

### *Umbellula thomsonii* Kölliker 1874

*U. thomsonii* Kölliker 1874*a*, p. 13.
*U. thomsonii* Kölliker 1874*b*, p. 10, Pl. 1, figs. 1–5.
*U. thomsonii* + *U. Güntheri* + *U. leptocaulis* + *U. simplex* Kölliker 1880, pp. 18–20, Pl. 9, figs. 34–36.
Non-*U. güntheri* A. Agassiz 1888, p. 314.
Non-*U. güntheri* Studer 1894, p. 57.
*U. crassiflora* Roule 1905, p. 456.
*U. intermedia* + *U. rosea* + *U. Köllikeri* Thomson & Henderson 1906, pp. 94, 95, 97, Pl. 5, fig. 5.
*U. Hendersoni* Balss 1910, p. 68, footnote.
*U. Güntheri* Broch 1913, p. 3, Pl. 1, fig. 1.
*U. thomsonii* + *U. güntheri* + *U. rosea* + *U. crassiflora* + *U. intermedia* + *U. simplex* Kükenthal 1915, pp. 52, 54, 56–58.
*U. aciculifera* J. Stuart Thomson 1915, p. 20, Pl. 2, fig. 2, text-fig. (on p. 21).
*U. Güntheri* Hickson 1916, pp. 120 *et seq.*
*U. aciculifera* J. Stuart Thomson 1923, pp. 49 *et seq.*
*U. güntheri* + *U. thomsonii* Deichmann 1936, pp. 268, 269.
*U. güntheri* Broch 1957, p. 351, Pl. 1, fig. 1, text-figs. 1–3.

This very characteristic species is easily identified by its three-flanged spicules (Broch 1913) and its strongly calcified, quadrangular rigid axis.

Discussing the synonymy of *U. güntheri* Kölliker 1880, I (Broch 1957) suggested the possibility that both *U. leptocaulis* Kölliker and *U. simplex* Kölliker (1880) had been founded on young specimens of *U. güntheri*. An examination of the original specimens in the British Museum has fully corroborated the suggestion.

In the same place (1957, p. 357) the position of *U. thomsonii* Kölliker 1874 was also touched upon, but owing to discrepancies in the different papers of Kölliker (1874*a*, 1874*b*, 1880) and the interpretations of Kükenthal (1915), I found the problem so confused that it was impossible to solve it without a study of Kölliker's types, although most statements indicated *U. güntheri* to be a synonym of *U. thomsonii*.

Kölliker based his descriptions of *U. thomsonii* on two specimens from the 'Challenger' Expedition (1880, p. 19, specimens A and B). The smaller specimen B could not be found in the collections of the British Museum;* according to Kölliker its height was 270 mm., but the specimen was defective. Specimen A has accordingly been selected as the lectotype of *U. thomsonii*. Kölliker wrote that the specimen was 895 mm. high and complete. However, the upper part with the autozooid cluster has now been broken off just below the swollen rachis. The upper limit of the holdfast cannot be ascertained with certainty, and the basal 'bulb' is contracted and not discernible.

Text-fig. 2 shows the position of the autozooids; it is a little at variance with the descriptions both of Kölliker (1874*a*, 1874*b*, 1880) and Kükenthal (1915). Originally there was one primary polyp (hatched in text-fig. 2) and twelve secondary autozooids, but two of the latter (stippled in text-fig. 2) had been cut away. The primary polyp and nine secondary autozooids are arranged in a whorl, and can be regarded as a direct continuation of the developmental sequence demonstrated by me (1957,

* Presumably the specimen was kept by Kölliker as a reward for working out the collection.

text-fig. 1) in *U. güntheri*. In addition to the autozooids forming the whorl, three fullgrown autozooids are found on the inner side of the ring, evidently displaced or pushed to the inner side of the whorl at intervals between autozooids of the outer circle. This displacement may possibly be due in part to a contraction of the rachis, especially in the case of the single displaced autozooid (unstippled in text-fig. 2). But the two inner autozooids on the other side are more likely to have budded inside the whorl. As far as we can judge from the literature, this specimen is the largest *U. thomsonii* examined up till now. This may explain the 'irregular' arrangement of the autozooids as compared with Broch's (1957) specimens. Probably very large clusters will be found to exhibit a more or less complete inner whorl of autozooids.

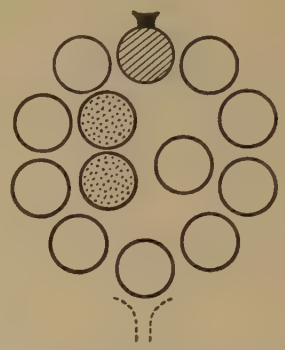

Fig. 2. *Umbellula thomsonii* Köll. (Specimen A, *lectotype*). Diagram of the arrangement of the autozooids in ventral aspect. The primary polyp hatched, the two autozooids which have been cut away stippled.

The re-examination of Kölliker's type thus confirms the synonymy of *U. thomsonii* and *U. güntheri*, and the first name must therefore have the priority.

(Lectotype: British Museum (Nat. Hist.) Reg. No. 1881. 2. 11. 23. Kölliker's Specimen A designated on p. 253, paragraph 4 as the lectotype).

## Non-spiculate species of *Umbellula*

In this second group of *Umbellula*, variations in, and contraction of specimens make the limitation of species exceedingly difficult, and specialists have wavered in their interpretations between a couple of species only, or a vast number, describing practically every new specimen as a new species. Here, of course, degrees of contraction have been welcomed as 'specific criteria'.

In these non-spiculate forms also, the shape of the axis is a comparatively reliable character, but again it is necessary to study the naked axis and not to judge by a superficial survey when the axis is enveloped in its more or less fleshy, inflated or contracted coverings.

Apparently nobody has studied the axis of the *Umbellula* species with the aim of determining the role of the calcareous incrustation. In taxonomic literature, among the specific characters often given is the possession of either a 'rigid', or a very flexible, stem. (It should be mentioned here that living pennatularians and their axes are throughout much more flexible than preserved specimens.) Where the calcareous incrustation of the axis is very scanty or almost wanting, the horny structure in some cases is rather more spongy than fibrous, and in such cases compression may distort it to a certain degree. The anatomical structure of the surrounding sheaths of the holdfast (or stalk) and their system of canals may then give the false impression that the axis was approximately quadrangular, and it is essential to make a critical study of the axis itself, its structure and the degree of calcareous incrustation.

The non-spiculate species fall into two groups: A, with a round axis, only very little if at all incrusted with lime, and B, with a quadrangular axis rather heavily incrusted with calcareous matter.

### *Group A*

Axis round, devoid of lime, very flexible.

*Umbellula huxleyi* Kölliker 1880 (Pl. 1, Figs. 1*a*, *b*)

*U. huxleyi* pars Kölliker 1880, p. 21, Pl. 9, figs. 37*a*, *b*.
*U. gracilis* A. M. Marshall 1883, p. 142, Pl. 25, figs. 29–35.
*U. huxleyi* Nutting 1909, p. 711.

*U. huxleyi* Kükenthal & Broch 1911, p. 290, Pl. 21, fig. 54.
*U. gracilis* Broch 1913, p. 6, Pl. 1, figs. 2, 3.
*U. huxleyi* + *U. gracilis* Kükenthal 1915, p. 53.
*U. huxleyi* Hickson 1916, pp. 122 seq.
Non-*U. huxleyi* Hickson 1937, p. 119.

This species was described by Kölliker from the 'Challenger' Expedition. In his report he mentions four specimens (A–D), one of which (C) is missing,* whereas the other three are in the collections of the British Museum (Nat. Hist.). The specimens, which according to their size and structure must be his A and B, have quadrangular axes; they are evidently young specimens of *U. lindahli*; they are discussed under this species on page 264. It is, however, quite clear that Kölliker really based his work on the largest specimen D, which he carefully described and figured. Specimen D has accordingly been selected as lectotype of *U. huxleyi*.

Kölliker wrote: 'Axis indistinctly quadrangular', evidently basing his definition on specimens A and B, caught in the same haul and assigned to the same species as D. (As mentioned above, these two specimens have now been assigned to *U. lindahli*.) The axis of the lectotype D is round throughout in section; the holdfast ('stalk'), which according to Kölliker is 34 mm. long, is also round. The axis is only very little thicker than the 'stem' and without any hint of quadrangularity. The thickening of the 'stalk' is due to greater development of the coenosarcal tissues which show some longitudinal wrinkles, suggesting a more or less angular section in the part shortly above the 'bulb'.

Kölliker assumed that the species was 'indistinctly bilateral in the fully developed stage'. Kükenthal (1915) on the other hand wrote: 'Die Zooide...stehen...am Schopfkelch dichter und nur ein dorsales Feld freilassend, gehen aber nicht auf das von den Polypen umschlossene innere Feld über'. In young specimens also this seems to be partly the case. Kölliker's type specimen D has no naked field dorsally between the siphonozooids on the swollen rachis below the autozooid cluster, and although siphonozooids are apparently absent between the bases of the autozooids in the lectotype, they have been observed in this position in larger specimens than those from the 'Challenger' and 'Valdivia' Expeditions. These two specimens are of about the same size, 180 and 193 mm., respectively, but the polyp clusters differ markedly in the development of their autozooids. The lectotype has 18 autozooids, ranging from mere buds to fully developed polyps; but a primary polyp is not distinguishable, and it is impossible to describe any arrangement in whorls. The 'Valdivia' specimen had only 6 autozooids. The dorsal one, which was a little smaller and placed a trifle above the circle, was considered to be the primary polyp; the autozooid to the left of the primary polyp was also a little smaller than the other four secondary autozooids. Nevertheless, the 'Valdivia' specimen evidently belongs to the same species as the 'Challenger' lectotype of *U. huxleyi*.

*U. gracilis* Marshall, from the 'Triton' Expedition, is also probably synonymous with this species although two of Marshall's statements might seem contradictory. He says (1883, p. 143): 'Stem cylindrical along the greater part of its length, becoming quadrangular in the terminal dilated part.' A glance at his drawing (1883, Pl. 25, fig. 29) shows at once that Marshall does not refer to the axis but to the entire stem and holdfast, and that he is really describing the longitudinal furrows caused by contraction of the ample tissues surrounding the lower and somewhat thickened part of the (round) axis. Marshall does not especially confine himself to the axis but uses the confusing phrase 'the stem or calcareous axis'. Here, however, we must remember that the four longitudinal main canals of the stalk-tissues (when contracted) always cause the thicker holdfast to appear more or less distinctly square, independently of the shape of the axis, whether round or square.

* See footnote, p. 253.

The other discrepancy lies in Marshall's introductory words, where he summed up the specific characteristics as 'distinctly bilateral'. However, his drawings (1883, Pl. 25, figs. 29, 30) clearly show that the bilateral arrangement of autozooids in the cluster is also quite rudimentary in his rather small specimen, and that, to cite his own words, 'it is difficult to make out any definite plan of arrangement of the polyps'.

Kölliker's specimen from the 'Challenger' and the statements of Kükenthal and Broch (1911) all indicate a similar rudimentary bilateral arrangement in young specimens of *U. huxleyi*, and Marshall evidently had a young stage of this species.

The large specimen of '*U. gracilis*' described from the 'Michael Sars' Expedition (Broch 1913) with a total length of 547 mm. had no less than 25 autozooids crowded together in the cluster which was almost globose (a pompon) because the polypiferous distal part of the rachis was extremely short. No bilateral arrangement of the autozooids could be traced, nor was it possible to point out any primary polyp because the axis did not run into the wall of any autozooid, but terminated in the swollen rachis.

In 1955 Dr A. R. Longhurst collected no less than 17 specimens of *huxleyi* in one haul with an otter trawl off Bissagos I. (Port Guiana) on a muddy bottom in 600 m. depth. This collection was generously placed at my disposal, and Dr Longhurst informed me that the comparatively large holdfasts ('stalks') of the specimens were rather strongly inflated and pulsating, when they came on deck. This is the first time apparently that pulsation has been observed in an *Umbellula*, and confirms the view that the lower part of the stem is, and also ought to be termed, a holdfast for digging into the mud.

Most of Longhurst's specimens measure about 27–28 cm. in length, three or four are a little shorter, as small as 18 cm. The specimens with two exceptions were stowed together and crushed into a container, so that it is impossible to count the autozooids in the clusters. Nevertheless, it can be seen that these agree with the polyp clusters described by Marshall (1883) and Broch (1913). Two specimens (Pl. 1, fig. 1*a*, *b*) had been picked out and preserved in a special glass container; they give an excellent impression of the specific characteristics.

The smaller specimen (*b*) has 14 fully developed autozooids and a 15th bud in the central part of the cluster. Eight of the autozooids constitute an outer (basal), somewhat irregular whorl, the others are crowded within this whorl and rather irregularly arranged. No primary polyp can be traced with any certainty, and with exception of the bud, the autozooids are of all but equal size. In the larger specimen (*a*), 10 autozooids constitute the outer (basal), very irregular whorl, and eight other autozooids of the same size are irregularly crowded within it showing no bilateral arrangement. It is impossible to trace a primary polyp. The largest autozooids of the outer whorl (excluding the tentacles) measure 17 mm. in length with a breadth of 3·5 mm. The autozooids of this specimen contain numerous eggs, whereas no eggs were observed in the smaller specimen.

Although of subordinate importance, it should be noted here that the tentacles of the preserved specimens are comparatively short in most adult autozooids, measuring $\frac{1}{3}$ to $\frac{1}{2}$ of the body length. In a few polyps the tentacles are more extended, being as long as or even longer than the body. The largest autozooids were found in the basal whorl. The dimensions are the same whether the specimens were filled with eggs or were sterile adult autozooids.

Symmetrical features are displayed with varying distinctness. In a few cases there is a strip without autozooids along the dorsal side of the swollen rachis, where it is possible to discern the almost hair-thin terminal part of the axis ending in the basi-dorsal wall of one of the autozooids, which is probably the primary polyp, although not differing in any way from the other autozooids. In every richer cluster, however, the upper part of the axis has been completely buried in the tissues of the rachis, and the polyp-free dorsal strip has disappeared completely; every trace of bilateral arrangement has

also been obscured by the larger clusters, the tightly packed autozooids being grouped on an extremely short terminal part of the rachis.

In these two best preserved specimens, siphonozooids were observed everywhere on the rachis, both between the autozooids and on the rapidly tapering part below the cluster. It was impossible to find any siphonozooids on the extremely thin upper part of the stem as well as on the holdfast.

The axis is extremely thin. In its upper part, immediately below the cluster, its diameter is scarcely 0·5 mm., nor does it increase until the middle of the stem is reached; from here downwards the axis slowly grows stouter and attains its greatest diameter—about 1 mm.—in the middle of the holdfast, tapering again towards the basal end. This entirely agrees with Marshall's observations, and with his remark that 'for the greater part of its length the stalk is extremely flexible, so much so that it can readily be coiled in circles of 5 mm. diameter without the slightest danger of breaking'. Although in live specimens the flexibility of the axis in most other deep-living, slender pennatularians is also great, such an extreme flexibility like that of *U. huxleyi* is very seldom encountered. It must be correlated with the extraordinarily scanty calcareous incrustation. On the other hand, the species has a very efficient holdfast, as shown by the photographs (Pl. 1, fig. 1). These two characters explain why the species has been reported from remarkably few localities, although its habitat, as collections show, is very extended and shallower than those of most other species of the genus.

Hickson's (1937) *U. huxleyi* with its rigid and quadrangular axis belongs to *U. pellucida* (see p. 261).

*U. huxleyi* is characterized by its obviously concentrated, pompon-like cluster, whereas the second spicule-free species *spicata* with a round axis is distinguished by the long, spaced tassel of very slender, long autozooids.

(Lectotype: British Museum (Nat. Hist.). Reg. No. 1881. 2. 11. 25. Specimen D of Kölliker, 1880.)

*Umbellula spicata* Kükenthal 1902 (Pl. 1, fig. 2)

*U. spicata* + *U. valdiviae* Kükenthal 1902, p. 594.

?*U. elongata* + *U. radiata* + *U. pendula* Thomson & Henderson 1906, pp. 96, 98, 99, Pl. 7, fig. 6.

*U. spicata* + *U. valdiviae* Kükenthal & Broch 1911, pp. 294, 295, Pl. 16, figs. 17–19, Pl. 20, fig. 51*a*, *b*; Pl. 21, figs. 52, 53.

*U. spicata* + *U. valdiviae* + *U. elongata* (?) + *U. radiata* (?) + *U. pendula* (?) Kükenthal 1915, pp. 53, 55, 57, fig. 60.

According to Kükenthal and Broch (1911), *U. spicata* and *U. valdiviae* differ as follows: *U. valdiviae* has a weak, more slender stem (this is not perceivable in the excellent figures). The rachis is not so contracted ('viel dicker') in *U. valdiviae* as in *U. spicata*. In *U. valdiviae*, the tentacle pinnulae alternate in size, whereas they increase successively in length towards the end of the tentacle in *U. spicata*. Neither of these features, which obviously are results of contraction, nor the differences in the arrangement of the siphonozooids mentioned in the detailed description, furnish a sufficient *fundamentum divisionis*. It must also be emphasized here that none of the specimens from the 'Valdivia' Expedition were adult.

In the collections at the British Museum (Nat. Hist.), an unrecorded specimen is labelled '1914. 1. 27. 1. Between Aden & Bombay, 13° N, 76° E, 600–700 fthms. J. E. Purton.' The specimen is broken, the lower part of the stem with the holdfast is in three pieces, whereas the upper part of the stem with the rachis and the large autozooid-tassel is comparatively very well preserved (Pl. 1, fig. 2). If these four fragments represent the entire specimen, its total length was about 55 cm., including the 9·5 cm. long rachis with its cluster of autozooids. In the lower part of the rachis the autozooids are placed in a couple of very indistinct whorls round the stem, but in the upper two-thirds or more, no regularity in the arrangement of the autozooids can be traced. These are separated by

comparatively large interspaces, especially on the lower part of the rachis, whereas all interspaces, as well as the tapering part of the rachis below the autozooids, are packed with comparatively prominent siphonozooids.

The autozooids are remarkably slender and long, in spite of the basal halves being filled with eggs. The length of the polyp body is up to 35 mm., but the breadth never exceeds 3 mm. The pinnulae do not show any features of taxonomic importance, their lengths evidently varying with the degree of contraction.

The salient feature of *U. spicata* as compared with *U. huxleyi* is the remarkable length of its rachis. This is very obvious on comparison of specimens in the photographs on Pl. 1, the autozooids of which are filled with eggs or larvae. The photographs also show that the reticulation of the surface of an autozooid does not depend on its being ripe, as was maintained by Hickson (1937, p. 120).

In the British Museum specimen the rachis occupies about 17% of the entire height, but in other specimens found hitherto it does not seem to be more than 10%. This long and slender rachis is thus a specific character, which however does not appear until, with growth, more autozooids have developed (cf. Kükenthal and Broch 1911, Pl. 16, fig. 19, and Pl. 20, fig. 51). In quite young specimens the autozooids show a bilateral arrangement, which however very soon disappears with the irregular budding of secondary autozooids on all sides of the rachis.

The British Museum specimen also presents other features which are of special interest. The upper part of the axis is round in section, but about the middle, or a little lower down, the axis is almost square, and this continues till the upper limit of the holdfast, whence the circular section continues to its lower end. It is remarkable that in the region with the square section the axis has an obviously loose structure and that calcareous incrustation seems to be completely wanting. This structure strongly recalls that of *U. huxleyi* and is evidently connected with the great flexibility of these specimens compared with species whose axes are rich in lime incrustation. The central core also of the axis in *U. spicata* is much looser in structure than the surface layer, and in some places below the middle length the axis even seems to have a central lumen. It is probable that such axes may become partially compressed into a square shape, by strong contractions of the sheath, e.g. when irritated by the unusual environment in the trawl, net, or when placed in preservative. This distortion has probably led some investigators to disregard the value of the normal shape of the axis as a taxonomic character. In *U. spicata* the British Museum mature specimen shows that a round axis with an extraordinarily loose or almost spongy structure in part, or even with a central lumen, is one of the specific characteristics.

It is probable that *U. elongata*, *U. radiata* and *U. pendula* Thomson and Henderson (1906) must be included among the synonyms of *U. spicata*, but the descriptions are so incomplete and expressed in such general terms, and the drawing of *U. elongata* is so schematic, that it is impossible to determine their identity without examination of the original material.

### *Group B*

Axis quadrangular, encrusted with lime.

In the second group of *Umbellula* without spicules the axis is quadrangular and strongly encrusted with calcareous matter. A long series of species has been described from all waters, together with the type species of the genus, the arctic *U. encrinus* (L. 1758), which seems to be confined to the deep waters of the Arctic Ocean, north of the ridges separating them from the Atlantic. *U. lindahli* Kölliker 1874 has been reported from the Atlantic Ocean, southwards from Greenland; *U. ambigua* Fischer 1889 (Marion 1906) from the central Atlantic; and more recently, *U. carpenteri* Kölliker 1880 has been shown to have a circumglobal habitat (Broch 1957). Kölliker described *carpenteri* from

Antarctic waters together with *U. magniflora* Kölliker 1880, and the 'Valdivia' Expedition brought back a third species, *U. antarctica* Kükenthal 1902, from the same area. Two species from the Indian Ocean were also erected in 1902 by Kükenthal, *U. rigida* and *U. pellucida*, and several other species have been added since that date.

Both Jungersen (1907) and Hickson (1907) expressed their doubts as to the validity of the three antarctic species *carpenteri*, *magniflora* and *antarctica*. Jungersen who gave careful details concerning *U. carpenteri*, wrote (1907, p. 9): 'es kommt mir deshalb als sehr möglich vor, dass diese Art nicht nur noch grösser wachsen, sondern höchst wahrscheinlich die Zahl der Polypen bedeutend vermehren und die ganze Form des Schopfes ändern mag, mit anderen Worten sich den Typus der *U. encrinus* (oder deren antarktischen Vertreters der *U. magniflora* = *U. encrinus* var. *antarctica* Kkth.) mehr näheren kann'. In 1937 Hickson was inclined to go yet a step further, and discard the shape of the axis as a specific criterion, considering all spicule-free Umbellulae as one species.

It is appropriate to consider here the distinguishing characters which have been used in this group. In his key Kükenthal (1915) gave them as follows:

| | | |
|---|---|---|
| 1. | Polypenträger kurz, Polypen annähernd in konzentrischen Kreisen stehend. | 2 |
| | Polypenträger lang, Polypen bilateral angeordnet. | 11 |
| 2. | Achse vierkantig. | 3 |
| 3. | Polypen ohne Spicula. | 4 |
| 4. | Tentakel ebenso lang oder länger als der Polypenkörper. | 5 |
| | Tentakel kürzer als der Polypenkörper. | 8 |
| 5. | Stock elastisch. | 6 |
| | Stock starr. | 7 |
| 6. | Kiel äusserst dünn. | *U. lindahli* |
| | Kiel relativ dick. | *U. encrinus* |
| 7. | Schopfkelch lateral abgeplattet. | *U. carpenteri* |
| | Schopfkelch dorsoventral abgeplattet. | *U. rigida* |
| 8. | Polypen zahlreich in mehreren konzentrischen Kreisen | 9 |
| | Polypen in geringer Zahl in einem Kreise. | *U. magniflora* |
| 9. | Polypen schlank und sehr gross. | *U. antarctica* |
| | Polypen dick, tonnenförmig und klein. | *U. pellucida* |
| 11. | Achse vierkantig. | 12 |
| 12. | Polypen ohne Spicula. | 13 |
| 13. | Tentakel lang. | *U. purpurea* |
| | Tentakel kurz. | *U. köllikeri* |

A glance at this key immediately raises the question: how to distinguish between the terms 'short' and 'long'? None of the species mentioned in it has a rachis comparable with that of *U. spicata*, the only one which can be characterized as 'long'. It is also questionable whether a difference exists between arrangement in approximately concentric whorls and bilateral arrangement. The young specimens in most species are more or less bilateral; the older specimens generally have fairly distinct whorls, concentrically arranged, sometimes indistinctly bilateral.

The other characters of the key in most cases are questions of degree or gradation, or are due to different stages of contraction. Some (e.g. point 5, whether the stem is rigid or elastic) might seem legitimate; however, the more specimens we investigate, the more difficult are the cases we run up against. Specimens are always more flexible when first caught than later on, and, of course, dry they are always much more rigid and brittle than if wet; in formalin or spirit their condition is intermediate between these two extremes. Rigidity is correlated to a certain degree with calcareous encrustation, with size of the specimens, etc. It must also be emphasized that flexibility evidently increases to some extent with the thickness of the sheathing tissue, as can be observed in typical colonies of

'*U. antarctica*'. To a great extent development of these covering tissues seems to depend on ecological conditions.

Characters like 'thin' as opposed to 'relatively thick' must be said to intergrade, and lateral or dorso-ventral compression is doubtless due to contraction; on the other hand in *U. pellucida* the shape of the autozooids is to some extent characteristic.

Hickson (1916) also discussed the question of distinguishing between the many species of this group. In general terms he gives his view as follows:

I. With a large number of autozooids (i.e. 40–50 in specimens of from 400–500 mm. in length) the autozooids being 20 mm. or more in body length.
   A. Tentacles much shorter. *U. antarctica*

II. With an intermediate number of autozooids (i.e. 15–40 in specimens 400–500 mm. in length).
   B. With a quadrangular axis. *U. encrinus, U. Weberi*

III. With a small number of autozooids (i.e. 8–15 in specimens 400–500 mm. in length).
   A. With tentacles longer than the bodies. *U. Carpenteri, U. Lindahli, U. loma*
   B. With tentacles shorter than the bodies. *U. Jordani, U. magniflora, U. pellucida*

It is evident that Hickson was of the opinion that the number of autozooids is comparatively constant in any single species of a certain length. Even allowing for the fact that as yet no specimen of e.g. *U. pellucida* as long as 400 mm. has been observed, the idea of a specific, characteristic, constant proportion between the length of the specimen and its number of autozooids is clearly disproved in my last paper (Broch, 1957 text-fig. 5), by the table of growth in *U. güntheri*, and again by the collections brought home by the Discovery Investigations.

In his key, Hickson only emphasizes in one place (II, B) the fact that the axis is quadrangular in two species of the group. Nevertheless, it is quadrangular in all species noted here in his table. The other character, the comparative length of body and tentacles in the autozooids, is of very little value because of the degree of contraction.*

Later on Hickson (1937) examined a great number of *Umbellula* from the Indian Ocean, which in spite of the quadrangular axis he named *U. huxleyi* Kölliker. Special attention was paid to the degree of contraction in relation to the sexual development of the autozooids, and Hickson came to the conclusion that 'it is obvious that pregnancy offers a physical impediment to contraction'.

It is usually quite easy to recognize the ripe from the barren autozooids without dissection, because the gonads in the former are clearly indicated by rectangular areas on the surface of the body wall. Such markings are clearly shown in Kölliker's figure (1880, pl. IX, fig. 37*a*) of *U. huxleyi*, and in Kükenthal and Broch's figure (1911, pl. XVI, fig. 17) of *U. spicata*. In the picture of *U. pellucida* (pl. XVI, fig. 20) by the authors of the 'Valdivia' Report the autozooids are strongly contracted, and there are no quadrangular markings on the body wall. No mention is made of the sexual condition of any of the species, but there can be little doubt that the two species, *U. spicata* and *U. pellucida*, are only ripe and barren forms of the same species, (according to Hickson).

It will suffice to point out that Kölliker's type specimen of *U. huxleyi* is a quite young, unripe *U. spicata* like Kükenthal and Broch's specimens of this species. The first known ripe specimen of *U. spicata* is figured in Pl. I, fig. 2; its surface is devoid of rectangular areas in the autozooids. The ripe specimen of *U. huxleyi* figured in Pl. I, fig. 1*a* also has smooth autozooids. Several specimens of '*U. huxleyi*' from the John Murray Expedition (re-examined by me in the British Museum (Nat.

* It might seem questionable, whether *U. loma* belongs to this group, because Nutting (1909) wrote that it has a few spicules on the swollen part of rachis below the polyp cluster, and one ought possibly to query it here. However, all other features suggest that the specimen is in its right place.

Hist.)) have autozooids packed with eggs, easily observable through the semi-pellucid, smooth body wall.

The examination of a very great number of spicule-free specimens shows that the proliferation and arrangement of the autozooids on the rachis afford specific characteristics, as indicated by Kükenthal and Broch in 1911. Later collections now give grounds for some further systematic regrouping.

In *U. spicata* as mentioned above, the rachis is remarkably long, and the autozooids bud irregularly. Siphonozooids of rather large size are crowded in the interspaces all over the rachis. Development results in a long, spaced tassel (Pl. I, fig. 2). Another more common developmental series is illustrated by *U. lindahli*. We might call it the *carpenteri–magniflora–antarctica* line. In the first stages the budding of autozooids shows a more or less distinctly bilateral arrangement, resulting in a ventral whorl lying distally on the rachis. Gradually the primary polyp is pushed into the central field of the whorl (or the upper part of the whorl dorsally encircles the primary polyp). During this '*magniflora* phase' the short proximal part of the rachis beneath the autozooid whorl generally takes the shape of a bowl on the top of the stem, and in the inner (upper) central field additional autozooids are budded in more or less indistinct whorls. At the same time the distal part of the rachis develops into a short spigot covered all over by autozooids, the bases of which are surrounded by large siphonozooids. This cluster can be regarded as a tassel, although much more concentrated than the *spicata* type. This *antarctica* (or *encrinus*) type is furnished with a distinct, generally rather regular, basal whorl of long autozooids (cf. Pl. II, fig. 6).

In some species, however, the budding of autozooids is restricted to the short distal end of the rachis, and so concentrated that the cluster is more correctly regarded as an almost globose pompon as in *U. huxleyi* (Pl. I, fig. 1) or *U. pellucida* (Pl. II, fig. 3). Here the autozooids often seem so crowded that no room is left between them for siphonozooids.

*Umbellula pellucida* Kükenthal 1902 (Pl. II, fig. 3*a*, *b*)

*U. pellucida* Kükenthal 1902, p. 593.
*U. purpurea* pars Thomson & Henderson 1906, p. 95.
*U. pellucida* Kükenthal & Broch 1911, p. 300, Pl. 16, fig. 20; Pl. 20, fig. 50*a–c*.
*U. pellucida* Hickson 1916, p. 134, Pl. 4, figs. 25, 26.
*U. huxleyi* Hickson 1937, p. 119.

This species is one of the small *Umbellulae*, none of the specimens (about 250) examined attaining a length of 350 mm. and only quite exceptionally exceeding 300 mm. The species is evidently comparatively common in the Indian Ocean, and prefers lesser depths than most other species of the genus, seemingly above 1600 m., although a single specimen has been caught at 2001 m. depth by the John Murray Expedition.

'The axis in all the specimens is quadrangular in section: that is to say, it is marked by four shallow longitudinal grooves with four prominent rounded ridges. At the stalk end the ridges become shallower, and for a considerable distance the axis becomes almost circular in section. The greatest width of the axis of a large specimen is 1 mm.', wrote Hickson (1937) who had at his disposal 249 specimens.

These words at once tell us that the specimens do not belong to *U. huxleyi*, and examination of these specimens in the British Museum (Nat. Hist.) at once confirmed that they belong to *U. pellucida*. The structure of the axis is quite different from *U. huxleyi*; it is abundantly incrusted with lime and compact throughout; the stem is therefore only slightly flexible, and in preserved specimens rather rigid and brittle like other species with square axes.

Kükenthal and Broch (1911) described the autozooids in *pellucida* as barrel-shaped. This will depend in part upon the degree of contraction, and Hickson's (1916) drawings show funnel-shaped

autozooids which are evidently much more extended than those of Kükenthal and Broch (again reproduced by Kükenthal 1915), which were drawn on board the 'Valdivia' from living specimens. The autozooid cluster strongly recalls that of *U. huxleyi*. The autozooids are small and crowded on to the short distal part of the rachis, and as Hickson (1937) pointed out, their arrangement varies so much from specimen to specimen, that in most cases it is impossible to trace any regularity. In larger clusters the numbers of autozooids commonly amount to some 25 to 30. In several specimens a naked narrow dorsal field along the axis gives an impression of certain bilaterality in the pompon.

The specimens from the German 'Valdivia' Expedition had a somewhat thicker basal holdfast, the length of which according to Kükenthal (1915) measured one-sixth to one-quarter of the entire stem. In most of the specimens from the John Murray Expedition, this part is so contracted transversely that it is impossible to trace an upper limit of the holdfast.

Young specimens of *U. pellucida* are probably difficult to distinguish from those of *U. lindahli* in some cases, but developmental stages of *U. pellucida* have hitherto escaped the collectors; probably their dimensions will be very tiny.

In his review Kükenthal (1915) stated that there were no siphonozooids between the autozooids of the cluster, but that they only occurred on the swollen part of the rachis below the cluster and in small numbers on the thin stem. External examination of some of the specimens from the John Murray Expedition, the siphonozooids of which are very obvious on the rachis below the cluster, showed that no siphonozooids could be detected between the autozooids. This feature seems to be constant and therefore *pellucida* differs from the following species, *lindahli*, where comparatively large siphonozooids are present between the autozooids of the cluster.

Thomson and Henderson (1906) described an *U. purpurea* with round axis from the Indian Ocean. A 'cotype' of it had been deposited in the British Museum (Nat. Hist.). This specimen has evidently been regarded as a younger stage of *purpurea*, described from a type specimen with no less than 53 autozooids arranged in 4 whorls+7 'at the tip that had no definite arrangement'. The cluster of the 'cotype' has only 11 autozooids, which measure some 5–6 mm. in length (without the tentacles). Eight of them, including the primary, largest polyp, are placed in one whorl, the last three in the central upper field within this whorl. All the autozooids are directed towards the ventral side of the specimen and give the entire cluster a decidedly bilateral appearance. The polyps are semi-pellucid and in all characters including the quadrangular axis recall *U. pellucida*; the axis obviously differs from the description of Thomson and Henderson. This cotype is evidently not *purpurea* but a rather young stage of *U. pellucida*. A renewed investigation of the type specimen of *purpurea* is needed to settle its identity.

*Umbellula lindahli* Kölliker 1874 (Pl. I, fig. 3, Pl. II, figs. 5, 6)

*U. miniacea*+*U. pallida* Lindahl 1875, pp. 12, 13, Pls. 1–3.
*U. lindahli* Kölliker 1874*b*, p. 11.
*U. carpenteri*+*U. magniflora* Kölliker 1880, pp. 23, 24, Pl. 10, figs. 38–40; Pl. 11, figs. 41, 42.
*U. Bairdii* Verrill 1884, p. 219.
*U. Bairdii* Verrill 1885, p. 509, Pl. 1, figs. 1, 2.
*U. ambigua* Fischer 1889, p. 37.
*U. encrinus* var. *antarctica*+*U. Köllikeri*+*U. rigida* Kükenthal 1902, pp. 595, 596.
*U. lindahli* Jungersen 1904, p. 75, Pl. 3, figs. 37–46.
*U. ambigua* Marion 1906, p. 146, Pl. 15, fig. 22.
*U. carpenteri* Hickson 1907, p. 12, Pl. 1, figs. 1–7.
*U. carpenteri* Jungersen 1907, p. 5, Pl. 1, figs. 1–10.
*U. encrinus* var. *ambigua* Stephens 1907, p. 21.

*U. Jordani* Nutting 1908, p. 564, Pl. 42, fig. 3.
*U. loma* + *U. magniflora* Nutting 1909, p. 710, 712, Pl. 87, fig. 9.
*U. antarctica* + *U. rigida* + *U. köllikeri* Kükenthal & Broch 1911, pp. 286, 292, Pl. 15, fig. 15; Pl. 26, fig. 16.
*U. magniflora* + *U. carpenteri* Nutting 1912, pp. 42, 43.
*U. carpenteri* Kükenthal 1912, p. 345, Pl. 23, fig. 22.
*U. lindahli* + *U. encrinus ambigua* + *U. carpenteri* + *U. rigida* + *U. antarctica* + *U. köllikeri* + *U. jordani* + *U. loma* Kükenthal 1915, pp. 48–50, 54, figs. 55–7.
*U. antarctica* + *U. Weberi* + *U. Jordani* Hickson 1916, pp. 128, 131, 133, Pl. 3, fig. 20; Pl. 4, fig. 24; text-fig. 29B, D, G.
*U. encrinus* var. *lindahli* Jungersen 1916*b*, p. 500.
*U. encrinus* var. *lindahli* Jungersen 1919, p. 1158.
*U. encrinus* var. *lindahli* Broch 1929, p. 149.
*U. lindahli* Deichmann 1936, p. 268.
*U. encrinus* Madsen 1948, p. 17.
*U. carpenteri* Broch 1957, p. 357, Pl. 1, figs. 2–4, text-figs. 4–6.

Under the name of *Umbellula carpenteri*, Kölliker (1880) gave a description of 5 specimens (A–E) from the 'Challenger' stations 156 and 157. Unfortunately, he did not say precisely from which station each specimen originated, and all of them have been merged in the same container. However, he mentioned that the specimens A–E exhibit 'a very interesting gradation from a bilateral to an apparently irregular arrangement of the polyps'. Kölliker probably used the largest specimen E as the main base for his description. Specimen C is lost, but the specimens A, B, D and E are in the British Museum (Nat. Hist.). All are figured in Kölliker's paper.

According to Kölliker, the type specimen E has eight polyps, arranged in the form of a rosette, and surrounding a ninth middle polyp like a cup; the axis terminated not in the ninth, but in one of the eight. It is, however, not possible to tell with certainty where the axis terminates if specimen E is examined. It does not end in the (dorsal) wall of the upper autozooid (see text-fig. 3, 1), but is bent inwards below its base, disappearing into the tissues of the rachis below the autozooids. This is the condition met with in *U. magniflora* (see below). Dissection would be necessary to determine whether the central, or the dorsal autozooid of the cluster is the primary polyp. In appearance the specimens resemble those from the Discovery collections which are intermediate between typical *carpenteri* and *magniflora* specimens.

In specimen D (Kölliker 1880, Pl. 10, fig. 39) all autozooids have contracted tentacles. In the same way as in *Cornularia* (Broch 1935) and *Solenopodium* (Broch and Horridge 1957) the tentacles seem to be laid together, stretched upwards and contracted like those of a slug by inverting the distal (oral) part of the body wall. It is interesting to note in this connexion that polyps with contracted tentacles have very seldom been found among over a hundred specimens of *Umbellula* which have passed through my hands. The specimen D (text-fig. 3, 2) has eight autozooids in one slightly irregular whorl. The conspicuously smaller, primary polyp is distinctly characterized by the terminal part of the axis running up to about the middle of its (dorsal) wall. The primary polyp has, on the other hand, been displaced a little to the inner side of the whorl, evidently by the outgrowth of the two adjacent secondary autozooids.

Specimen B (length 105 mm.) figured by Kölliker (1880, Pl. 10, fig. 39*a*) has 3 autozooids, the median of which is the primary polyp, the axis continuing in its (dorsal) wall till about one-third below the tentacle bases; there is a small knob where it terminates, but there seems to have been no free end of the rachis. The specimen differs a little from the youngest developmental stages from the Swedish Deep-Sea Expedition (Broch 1957), but corresponds with two small specimens from Discovery St. 181.

Specimen A which is only 51·5 mm. long, also has been figured by Kölliker (1880, Pl. 10, fig. 39*b*). His description runs: 'Four polyps, all lateral with a free end of the rachis, are visible in fig. 39, C.' The letter C must be due to a slip of the pen. The specimen is figured in dorsal (in Kölliker's terminology 'ventral') view. It seems to have escaped Kölliker's attention that a small but undeniable autozooid bud is placed ventrally between the two figured median autozooids (Pl. I, fig. 3); the cluster thus has 5, not 4 autozooids. This, however, does not alter Kölliker's implication in the text that no primary polyp can be traced. On the other hand, the obvious, free end of the rachis strongly recalls the young stages from the Swedish Deep-Sea Expedition, although in these a primary polyp is clearly to be seen (Broch 1957).

The Challenger collection in the British Museum (Nat. Hist.) also contains two more young stages of the species *lindahli*, viz. the two smaller specimens assigned by Kölliker to *U. huxleyi* (see p. 255). Their quadrangular axes differ from this species, and also their other features show that they belong to the same species which Kölliker thoroughly described under the name of *U. carpenteri*.

Kölliker (1880, p. 24) instituted another, new species, *U. magniflora*. Here the rachis is bowl-shaped, and as far as can be discerned in the type specimen, which is in a rather bad state, the axis enters from below centrally. It is impossible to see where it terminates, and it is also not possible to tell which of the autozooids might be the primary polyp. The arrangement of the autozooids (text-fig. 3, 3) is very like that in a specimen from 'Discovery' St. 371 with a total length of 46 cm. (Table, p. 266 no. 5). Kölliker's type has an outer whorl of 9 autozooids along the brim of the 'bowl' and in the centre, within it, one central autozooid of the same size as the marginal autozooids; finally, there is also one polyp bud below it as indicated in text-fig. 3, 3. Because of the brittleness of the specimen I did not venture upon a more thorough investigation. This specimen is without doubt only an individual variant, or growth form, of '*U. carpenteri*', a variant rather common among the specimens from subantarctic-antarctic waters, which are a little larger than those examined and mentioned by Hickson (1907) and Jungersen (1907) under the name of *U. carpenteri*. The size of Kölliker's specimen (740 mm. total length) corresponds with the smaller specimens of the '*magniflora*' stage from the Discovery collections.

A third antarctic *Umbellula* was announced in a preliminary paper by Kükenthal (1902) as *U. encrinus* var. *antarctica*. In his paper on *U. carpenteri* from the Belgian Antarctic Expedition, Jungersen (1907) hints at the possibility of all three antarctic *Umbellula* species being synonyms: 'es kommt mir deshalb als sehr möglich vor, dass diese Art nicht nur noch grösser wachsen, sondern höchst wahrscheinlich die Zahl der Polypen bedeutend vermehren und die ganze Form des Schopfes ändern mag, mit anderen Worten sich den Typus der *U. encrinus* (oder deren antarktischen Vertreters der *U. magniflora* = *U. encrinus* var. *antarctica* Kkth.) mehr nähern kann.' Kükenthal and Broch (1911), and Kükenthal (1915) raised the variety to a separate species *U. antarctica*, and Kükenthal distinguished between three antarctic species, viz. *U. carpenteri*, *U. magniflora* and *U. antarctica*.

The following table gives a list of the specimens from the Discovery collections:

| *Station* | *Depth (m.)* | *Remarks on the specimens* |
|---|---|---|
| 180<br>11 March 1927<br>Palmer Archipelago | 160 | One specimen: total height 67 cm.<br>3–4 irregular whorls of autozooids. The axis enters the centre of the bowl-shaped basal part of the rachis. Siphonozooids in all intervals between the autozooids, some of them with half extended tentacles. In spite of a very thin stem it is a typical *antarctica* specimen. |
| 181<br>12 March 1927<br>Palmer Archipelago | 160–335 | 6 specimens.<br>1 and 2, total height 7·5 cm.<br>Both have only one pair of fully developed secondary autozooids, but whereas 1 only shows the first traces of a lower pair, in 2 this is seen as small buds (text-fig. 3, 4). The |

| *Station* | *Depth (m.)* | *Remarks on the specimens* |
|---|---|---|
| 181<br>12 March 1927<br>Palmer Archipelago<br>(*cont.*) | 160–335 | terminal part of the axis ends in the dorsal wall of the primary autozooid, but does not project spine-like (cf. Broch 1957). The axis is very thin but distinctly quadrangular.<br>3, total length 47 cm.<br>The primary polyp has been pushed to the inner side of the whorl by the dorsal secondary autozooids (text-fig. 3, 5). Siphonozooids distinct between the autozooids, a few with extended tentacles. Autozooids: body up to 2 cm., tentacles 1–2 cm. (In spite of the much greater size, the cluster of the specimen has only one autozooid more than the 14·8 cm. specimen figured by Jungersen (1907, Pl. 1, figs. 1, 2), with which it otherwise agrees except in size of bodies of the autozooids which, according to Jungersen, measure only up to 8 mm.).<br>4, total length 90 cm.; 5, total length 93 cm.<br>The specimens were labelled *U. magniflora* by Mrs MacFadyen; they are in a bad state of preservation, but evidently showed the same features as specimen 6.<br>6, total length 98 cm.<br>In its upper part the axis is only 1·5 mm. thick and enters the centre of the bowl-shaped 'bottom' of the rachis, but from here it runs along the outer wall of the rachis to its brim, terminating at the base of an autozooid seated on the inner side of a whorl of 15 secondary autozooids. Inside this whorl the rachis is crowded by siphonozooids and seems hirsute because of the extended tentacles. Some of the siphonozooids of the lower side of the rachis also have extended tentacles. Typical *magniflora*. |
| 182<br>14 March 1927<br>Palmer Archipelago | 278–530 | One specimen: total length 105 cm.<br>Lower part of rachis bowl-shaped, axis entering its centre from below and disappearing. A few of the external siphonozooids have extended tentacles. 12 autozooids form a whorl along the brim, 3 more autozooids in the central upper field of the 'bowl'; the field is covered with hair-like tentacles of otherwise invisible siphonozooids. A primary polyp cannot be located. Some of the autozooids show the following lengths of body + tentacles in mm.; 4+4; 4+3·5; 3·5+4; 3·5+2·5; 3+2·5. Typical *magniflora*. |
| 366<br>6 March 1930<br>S. Sandwich Is. | 77–152 | 7 specimens.<br>1, total length 24 cm.<br>The axis enters the centre of the broadly obconic basal part of rachis from below and disappears. 10 large autozooids (body up to 17 mm., tentacles to 22 mm. long) constitute a basal whorl, and within it there are two additional irregular whorls of large autozooids. The basal whorl recalls *magniflora*, but the additional autozooid whorls transform the cluster into *antarctica*.<br>2, total length 43 cm.<br>Both autozooid bodies and tentacles up to 25 mm. long. Basal part of rachis bowl-shaped, axis entering centrally and disappearing. One lower (marginal) whorl of 11 autozooids, within it on a short spigot 3 irregular whorls. All interspaces between the autozooids crowded with rather prominent siphonozooids with withdrawn tentacles. Typical *antarctica* with the basal part of rachis like that of *magniflora*.<br>3, total length 45 cm.<br>Strongly twisted just below the cluster. Both autozooid bodies and tentacles up to 3 cm. Axis entering centrally from below, thence following the (dorsal) wall to disappear in an interspace between two autozooids of the basal whorl. This consists of 11 polyps. Within and above it, numerous crowded autozooids in 3–4 indistinct, very irregular whorls. Siphonozooids in all interspaces between the autozooids, always with retracted tentacles. Typical *antarctica*.<br>4, total length 73 cm.<br>Axis diameter about 2 mm. just above the holdfast, only 1 mm. near the cluster. Basal part of rachis bowl-shaped, axis entering the centre from below and disappearing. 9 fully developed autozooids along the brim of the 'bowl' in a single whorl, a tenth indicated by a bud. Diametrically opposite the bud one fully developed autozooid (the primary polyp?) is seated on the inner side of the whorl. Autozooid bodies 1·5–2 cm. long. Siphonozooids on the 'bowl' below the autozooids seemingly crowded into radial fields, no siphonozooids visible inside the autozooid whorl. Typical *magniflora*.<br>5, total length 86 cm.<br>Axis as in 4, entering the bowl-shaped basal part of rachis in the centre from below, but abruptly making a bend to one (the dorsal?) side and following the wall to the brim. There are 10 autozooids in a whorl round the brim of the 'bowl', and the axis lies in a narrow, |

| *Station* | *Depth (m.)* | *Remarks on the specimens* |
|---|---|---|
| 366<br>6 March 1930<br>S. Sandwich Is.<br>(*cont.*) | 77–152 | deep furrow between the two (dorsal) secondary autozooids, then again it bends a little inwards to end in the basal wall of an eleventh autozooid (the primary polyp), which has been displaced to the inner side of the whorl (text-fig. 3, 7). Autozooid bodies 2–2·5 cm., tentacles 1·5–2 cm. long. Siphonozooids evidently placed like those of 4, but all but invisible. Typical *magniflora*.<br>6, total length about 100 cm.<br>Rachis bowl-shaped with 11 marginal autozooids and one a little smaller (primary polyp?) near the centre of the whorl. The axis enters the centre from below and disappears. Siphonozooids numerous on the lower side of rachis, not visible within the whorl of autozooids. Tentacles retracted.<br>7, total length about 107 cm.<br>Rachis like that of 6, surrounded by a whorl of 10 autozooids. In the central field there are two additional autozooids of the same size. Siphonozooids only visible on the lower part of rachis, some of them with extended tentacles. Both in 6 and 7 the stem is exceedingly slender and flexible, the upper part of the axis just below the rachis does not attain a diameter of 1 mm., and shortly above the holdfast it is only 1·5 mm. thick. |
| 371<br>14 March 1930<br>S. Sandwich Is. | 99–161 | 6 specimens.<br>1, total length 31 cm.<br>Specimen rather 'fleshy', but with a thin axis, measuring just below the cluster 0·7 mm., shortly above the holdfast about 1 mm. thick. Rachis basally laterally compressed by contraction. Autozooids in 3–4 quite irregular whorls, young and small autozoids budding irregularly between the large ones. Although rather strongly contracted the larger autozooids with body lengths up to 20 mm. and tentacles 8–10 mm. long. Siphonozooids in all interspaces between the autozooids, with retracted tentacles.<br>2 and 3, total length in both about 37 cm.<br>Both specimens rather fleshy. Axis just above the holdfast about 2 mm., below the rachis 1 mm. thick. Autozooids with body lengths up to 4 cm., tentacles to 2 cm. Both the tissues of the polyps and those of the wrinkled and folded stem and holdfast are not distinctly contracted but are remarkably flaccid. 2, has some 37 autozooids, the 9 lowermost of which constitute a whorl round the bowl-shaped basal part of rachis. 3, has 12 autozooids in the basal whorl of the ample tassel. Both specimens link *antarctica* together with *rigida* (cf. Kükenthal and Broch 1911, Pl. 26, fig. 16).<br>4, total length 43 cm.<br>The specimen is fleshy, the coenenchyma wrinkled and folded although seemingly not very contracted. Axis 3 mm. thick just above the holdfast, 1·8 below the cluster. Rachis was bowl-shaped below the cluster, but is now (by preservation?) strongly wrinkled. The axis enters the rachis in the centre from below and disappears. The cluster has more than 40 autozooids with bodies up to 4 cm. and tentacles mostly 1·5–2 cm. long. Young polyps and new buds irregularly scattered among the fully developed autozooids. Siphonozooids crowded in all interspaces between the autozooids as well as on rachis below the cluster, none with extended tentacles.<br>5, total length 46 cm.<br>Rather slender, axis just above the holdfast 1–1·5 mm., just below the cluster $\frac{3}{4}$ mm. thick. The basal part of rachis is nearly bowl-shaped. The axis enters it centrally from below, but here it bends and follows one (dorsal) side ending in the basi-dorsal wall of one (primary) autozooid. There are 8 fully developed secondary autozooids in one simple whorl along the brim of the bowl-shaped rachis; a small ninth bud diametrically opposite the primary polyp. This has been pushed to the inner side of the whorl (the cluster almost coincides with text-fig. 3, 7). The autozooids are rather inflated and show body lengths up to 3 cm., whereas the rather contracted tentacles at most are 1·2 cm. long. Siphonozooids indistinctly observed in all spaces between the autozooids. Typical *magniflora*.<br>6, total length 88 cm.<br>Very slender, axis near the holdfast 1·5 mm., just below the cluster $\frac{3}{4}$ mm. thick. Autozooids contracted but not externally wrinkled, body up to 2 cm., tentacles up to 5 mm. long. Siphonozooids in all interspaces between the autozooids, almost invisible, also crowded on the under side of the bowl-shaped rachis. 10 autozooids in a simple whorl and an eleventh displaced to the inner side on one (the dorsal?) side. The cluster agrees with 5 from St. 366 (text-fig. 3, 7) but the terminal part of the axis is buried in the tissues of the rachis. |

| *Station* | *Depth (m.)* | *Remarks on the specimens* |
|---|---|---|
| 1644<br>16 January 1936<br>Ross Sea | 645 | 1 specimen, total length 15·5 cm.<br>The cluster has 5 large autozooids and 4 equal buds, the positions of which are evident from text-fig. 3, 6. The arrangement is obviously bilateral, but the displacement of the primary polyp by the budding of the two dorsal autozooids indicates the development of a bowl-shaped rachis. Siphonozooids are crowded in all interspaces between the autozooids as well as on the tapering basal part of rachis below the cluster, many with tentacles extended. |
| 1645<br>17 January 1936<br>Ross Sea | 435 | 1 specimen, total length 55 cm.<br>The lower part of rachis is bowl-shaped with 11 fully developed autozooids along the brim. Inside the whorl one fully developed autozooid is seated near one side, and evidently two buds are developing near the other side. The central field appears covered by hairs because of the extended tentacles of the siphonozooids, which also give the part of the rachis below the autozooid whorl a shaggy look. Between the autozooids of the whorl no siphonozooids were visible. |
| 1652<br>23 January 1936<br>Ross Sea | 567 | 1 specimen, total length 36 cm.<br>Axis just above the holdfast 1 mm. thick, just below the cluster $\frac{3}{4}$ mm. thick. Autozooids with bodies up to 3 cm., tentacles up to 2·2 cm. long. One whorl consisting of 7 full-grown autozooids and one small bud; in the inner field one excentric, large autozooid. Siphonozooids all over the rachis, tentacles retracted. Typical *magniflora*. |
| 1948<br>4 January 1937<br>S. Shetland Is. | 490–610 | 3 specimens.<br>1, total length 36 cm.<br>The comparatively distinct holdfast is about 6·5 cm. long and rather fleshy like the stem. Axis just above the holdfast 2 mm. thick, just below rachis 1 mm. thick. It enters the centre of the broad obconical basal part of rachis and disappears in the tissues. Autozooids moderately contracted, body up to 2 cm., tentacles up to 1·7 cm. long. Five full-grown individuals and one bud make up a basal whorl of autozooids. Within and above it 3–4 quite irregular crowded 'whorls' of autozooids are developed, and in all interspaces between them and on rachis below the tassel, siphonozooids are thickly placed, some of them with extended tentacles. Typical *antarctica*.<br>2, total length 37 cm.<br>Holdfast about 8·5 cm. long, with dimensions as in 1. Holdfast and stem fleshy. Autozooids moderately contracted, body length up to 2·5 cm., tentacles to 2 cm. There is a basal whorl of 11 autozooids, and 4–5 quite indistinct and irregular 'whorls' on a short spigot within the basal whorl. Here as in 1 the autozooids of the inner 'whorls' are a little smaller than those of the base. Siphonozooids, often with extended tentacles, are crowded between the autozooids and all over the rachis. Here as in the following 3 the basal part is that of a typical *magniflora*, but the upper 'whorls' of the tassel have changed the specimen into a typical *antarctica*.<br>3, total length 38·5 cm.<br>Holdfast contracted, about 9 cm. long, axis dimensions agreeing with 1 and 2. Specimen fleshy. The upper part of the stem just below the cluster is strongly curved owing to contractions of the coenenchyma. The basal whorl of the tassel consists of 11 flaccid autozooids with bodies up to 3 cm. and tentacles up to 2 cm. long. The distal part of the tassel is packed with irregularly placed, somewhat smaller autozooids, and all interspaces between them are crowded with siphonozooids, some of them with extended tentacles. Between the autozooids several new buds are observed. |

The Discovery collections contain no less than 26 specimens of different sizes from antarctic waters which furnish a good basis for a discussion of the problem (Table, pp. 264 to 267).

The smallest specimens (St. 181) are only 7·5 cm. long and besides the primary polyp they have one pair of fully developed secondary autozooids and below them a pair of autozooid buds (text-fig. 3, 4). Thus they correspond to Broch's (1957) text-fig. 4, III, and text-fig. 5, no. 5 (*Umbellula carpenteri*), although the rachis does not jut out above the primary polyp and the buds are placed a little below the first pair of secondary autozooids. This probably is the 'normal' case.

In a third specimen from St. 181 (text-fig. 3, 5) with a total length of 47 cm., a third pair of autozooids has evidently been developed at the dorso-lateral sides of the primary polyp, or the rachis has been thickened a little at the same time as a lower (more ventral) pair has pushed the upper pair more

to the dorsal side of the primary polyp. A specimen from St. 1644 (total length 15·5 cm., text-fig. 3, 6) shows that new buds may also arise on the dorso-lateral sides of the primary polyp (i.e. also on the axis), ventrally between, or a little below, the lowermost pair of secondary autozooids.

This development leads to the formation of a cluster like that figured in text-fig. 3, 7 from a specimen with total length 86 cm. (St. 366, no. 5 of the table). Here the lower part of the rachis has a bowl-like shape, and the secondary autozooids are situated along its brim. The axis enters the centre of the bowl at the bottom, but from here it follows the dorsal side of the rachis in a deep and narrow furrow to the brim between two dorsal secondary autozooids, bends inwards and ends in the basi-dorsal wall of the primary polyp, which has been displaced into the central field by the growth of the whorl of secondary autozooids.

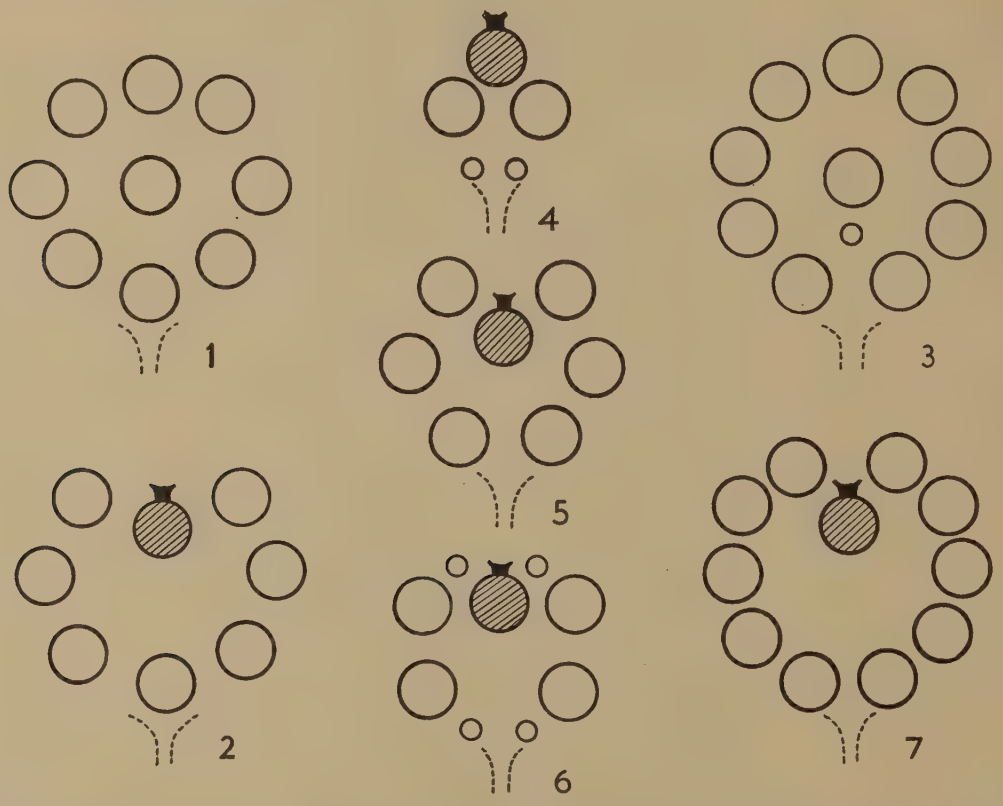


Fig. 3. *Umbellula lindahli.* Diagrams showing the arrangements of autozooids in clusters with comparatively few polyps. Where distinguishable the primary polyp is hatched. 1. Type specimen E of *Umbellula carpenteri* Kölliker, 1880. 2. Kölliker's specimen D of the same species. 3. Type specimen of *Umbellula magniflora* Kölliker, 1880. 4. Two small specimens from *Discovery* St. 181 (nos. 1 and 2 of the table, p. 264). 5. *Discovery* St. 181, no. 3 (p. 265). 6. The specimen from *Discovery* St. 1644 (p. 267). 7. *Discovery* St. 366, specimen no. 5 (p. 265).

In other specimens this dorsal furrow has disappeared because of the growth of the rachis-tissues and can only be made out by dissection. Here we might speak of typical *magniflora* specimens, when only some few further autozooids have developed in the central field. The type specimen of Kölliker's (1880) *magniflora* (text-fig. 3, 3) evidently shows the commencement of the development of such clusters.

On the other hand, we cannot look on this development of the cluster as absolutely characteristic of the species. In several cases the primary polyp and the axis retain their peripheral dorsal position, and the entire cluster in the main keeps its predominantly ventral position on the rachis, with generally

also a more or less distinct bilateral structure. In these specimens the rachis below the autozooids generally retains a more slender and obconical shape in preserved specimens, although we also find stages, where the rachis is more fleshy, or less strongly contracted. This development leads to the formation of polyp-clusters like those of the largest specimens from the Swedish Deep-Sea Expedition (Broch 1957, text-fig. 4, VII). In that paper the possibility was indicated, that such clusters with two whorls of autozooids may give the final and normal arrangement of the species, as found in specimens with total heights of 105 and 119 cm. This, however, is not the case in antarctic waters. In the *magniflora* type especially, there is a tendency for several autozooids to develop in the central field within the first whorl of secondary autozooids. Great crowding results and arrangement in whorls is soon lost. At the same time the inner part of the 'bowl' develops into a spigot carrying autozooids on all sides. In typical *antarctica* forms, like those from St. 1948 (see also Pl. 2, fig. 6), these features are distinct, and in the largest of them (total height 38·5 cm.) new autozooids are budded everywhere between the old ones. Evidently the number of autozooids in the cluster in some way or other depends on local conditions rather than on hereditary fixed characters. On the other hand, collections like those from Stns. 366 and 371 indicate that specimens may develop divergently in one locality. Great individual variations can occur under apparently uniform conditions.

No correlation exists between total length and number of autozooids in the specimens, when they have passed their first stages of development. The specimen described by Kükenthal and Broch (1911) as the type of *U. antarctica* was rather short (total length 465 mm., a cotype 460 mm.); on the other hand, its 'stalk' (both holdfast and stem) is remarkably fleshy. Although this is the case in many specimens of typical *antarctica* forms, comparatively slender specimens with very thin coenosarc on stem and holdfast, but with typical *antarctica* clusters, also occur fairly frequently. In most cases such slender specimens have fewer autozooids in their clusters, which vary from the bilateral *carpenteri* to the radial *magniflora* type. The collections corroborate the suggestion of Hickson (1907) and of Jungersen (1907) that all antarctic *Umbellulae* with square axes and without spicules (apart from the calcareous concretions in the inner tissues of the terminal part of the holdfast) belong to one very variable species.

A study of the descriptions of other non-spiculate species of *Umbellula* with square axes shows that it is exceedingly difficult to trace differences, which might serve as reliable *fundamenta divisionis*. Many so-called characters are due to contraction; others to a certain degree are apparently dependent on local conditions. Polyp clusters have a tendency to develop more autozooids in subantarctic-antarctic as well as in subarctic-arctic seas, i.e. in colder areas, than in temperate and tropical waters. One might suggest that this is not only due to lower temperature, but also to an admixture of water from melting ice, i.e. to variations in salinity. In these colder seas, *Umbellula* is also found at much shallower depths than elsewhere. It is accordingly necessary to be most cautious in using the numbers of autozooids in the clusters for specific determination, because these numbers show no correlation with the length of the specimens (Broch 1957).

It has been mentioned earlier that Kükenthal was at first inclined to look on *U. antarctica* as a variety of *U. encrinus*. Later on he (1915) reduced *U. ambigua* Fischer (also retained by Marion (1906) as a separate species) to a variety of *U. encrinus*. This course was already indicated by Jane Stephens (1907), who had no less than 17 specimens at her disposal, the stems of which (from the clusters downwards) ranged from 112 to 420 mm. (Marion's specimen measured in the same way was about 350 mm.). The numbers of autozooids in the clusters varied from 6 to 43, and the polyp bodies from 8 to 30 mm. Marion's drawings (1906, Pl. 15, fig. 22, and 22 A) might well have been made from a typical specimen of *U. magniflora* Kölliker, and in his text Marion (1906, p. 146) writes: 'L'*Umbellula ambigua* se rapproche intimement de l'*Umbellula grandiflora* Kölliker prise dans l'Extrême-Sud, aux iles

Kerguelen. Cette curieuse affinité mérite d'être remarquée.' (By a slip of the pen Marion has written *grandiflora* instead of *magniflora* as his particulars prove.) There are no differences between Marion's and Kölliker's descriptions, and the Discovery specimens also coincide with them. It might be objected that Marion's specimen has a much shorter stem than the 'Challenger' specimen (measured in the same way as Stephens's specimens, the stem of Kölliker's specimen is some 690 mm.). Stephens, however, in her table gave measurements of a variation of '*ambigua*' quite parallel to that of *U. thomsonii* (Broch 1957 '*U. güntheri*'), additional evidence against the use of length of the stem (or total length of the specimen) as compared with the numbers of autozooids in the clusters for specific identification.

Finally, it is impossible to trace any distinct limit or difference between the typical *U. carpenteri* and the species *U. lindahli* (comp. Kölliker 1880, Jungersen 1904, 1907, and Broch 1957).

It is also necessary to discuss the relations between *U. lindahli* Kölliker (1874) and *U. encrinus* (L. 1758). Jungersen (1904, 1907) dealt partly with the question but although he considered them to be different species, he omitted to define their characteristic differences precisely and only hinted at their varying dimensions.

Summing up the characters stated by Kükenthal (1915) the following differences appear: (1) *U. lindahli* has a very long and thin stem, whereas the stem of *U. encrinus* is not especially thin. (2) The autozooids of *U. lindahli* are gathered in a slender cluster and occur in smaller numbers than in the much more robust clusters of *U. encrinus*, but the arrangement of the polyps otherwise agrees. (3) The tentacles of the autozooids of *U. lindahli* are twice as long as the polyp body, in *U. encrinus* of about the same length as the body. (4) In *U. lindahli* siphonozooids constitute two longitudinal rows along the thin part of the stem, in *U. encrinus* they are arranged all round it, and the coenosarc is thicker and more fleshy than in *U. lindahli*. The differences under (2) and (3) can at once be discarded as being due to contraction; (4) is correlated with a more or less copious individual development of the coenosarc, a fact clearly evident in the specimens from the Discovery collections.

Jungersen (1904) in his first paper came to the conclusion that *U. encrinus* must be regarded as a distinct species apart from *U. lindahli*, although differentiation was difficult. After the examination of new supplementary collections (1916*b*, 1919) he decided that *lindahli* and *encrinus* represent two varieties of one species, the older, Linnean name, *encrinus* having priority. This view was also accepted by myself (Broch 1929) in my review of the Arctic Octocorals where I mentioned the two groups as *U. encrinus* forma *typica* and forma *lindahli*.

Although there are no definite limits between the other 'species' amalgamated here under the name of *U. lindahli*, a somewhat greater gap apparently separates *U. encrinus* from the rest. It is of course necessary to make reservations when dealing with characters which may be correlated with the dimensions of the coenosarc, or which are largely due to contraction. The obvious parallel development in both cold-water areas must be considered: in extreme cases theoretically this should lead up to *U. encrinus* from *U. lindahli*. It would then be correct to consider *encrinus* as an ecologically distinct geographical form of *lindahli*. However, although at present it is difficult to define the limits exactly, I prefer to treat *encrinus* as a separate species. Probably the gap between the two 'species' emphasized by Jungersen (1904) is due to the limits and differences between the Atlantic and the Arctic deep-sea areas. Their size differs so greatly that it is generally easy to distinguish between specimens of the two 'species'.

## Zoogeographical remarks on *Umbellula*

As an introduction to the distribution of the species, all known localities are listed in the following table:

*Umbellula durissima* Kölliker

Pacific Ocean

34° 07′ N, 138° 00′ E, 1030 m., bottom temp. 2·3° C. (Kölliker 1880, type locality)
Shio Misaki Light, Japan, N 82° E, 12·5 miles, 1092 m. (*eloisa* Nutting)

Indian Ocean

10° 06′ N, 92° 29′ E, 1300 m. (*dura* Thomson & Henderson)
03° 27′ S, 131° 00′ E, 567 m.
Off the Laccadive Is, 2070 m.

Atlantic Ocean

02° 26′–02° 24′ N, 39° 26′–39° 12′ W, 4474–4430 m.
48° 06′ S, 10° 5′ W, 3188 m.

Antarctic

68° 06′ S, 10° 05′ E, 3185 m.

*Umbellula thomsonii* Kölliker

Atlantic Ocean

35° 20′ N, 13° 04 W, 3768 m. (Kölliker 1880, type locality)
Off Morocco, 2000 and 2125 m.
29° 08′ N, 22° 53′ W, 5160 m.
30° 19′–30° 30′ N, 55° 56′–56° 19′ W, 5600–5340 m.
12° 22′–12° 13′ N, 52° 00′–51° 44′ W, 5044–5033 m.
01° 47′ N, 26° 46′ W, 3380 m.
Guadeloupe ('Blake' St. 162) 1336 m.
28° 54′ N, 26° 46′ W, (?)
24° 12′–24° 28′ N, 63° 23′–63° 18′ W, 5850–5860 m.
01° 03′–00° 58′ N, 18° 40′–18° 37′ W, 5250–5300 m.
Cape Point NE by E ¼ E, 46 miles, 183–1647 m. (*aciculifera* St Thomson)

Indian Ocean

11° 58′ N, 88° 52′ E, 3190 m. (*rosea* Thomson & Henderson)
06° 52′ N, 81° 11′ E, 3500 m. (*intermedia* Thomson & Henderson)
12° 20′ N, 85° 08′ E, 3290 m. (*hendersoni* Balss)
04° 56′ N, 80° 52′ 30″ E, 3240 m.

Pacific Ocean

13° 50′ S, 151° 49′ E, 4460 m. (*leptocaulis* Kölliker)
36° 10′ N, 178° 00′ E, 3750 m. (*simplex* Kölliker)

*Umbellula huxleyi* Kölliker

Pacific Ocean

34° 71′ N. 135° 39′ E, S. of Yeddo (Japan), 1034 m., bottom temp. 3·3° C. (Kölliker 1880, type locality)
32° 50′ 20″ N, 118° 03′ 30″ W, 915 m.

Indian Ocean

S.W. of Great Nicobar, 296 m.

Atlantic Ocean

59° 29′ 30″ N, 07° 13′ W, 1032 m.
Off Bissagos I. (Port Guiana), 600 m.
28° 08′ N, 13° 35′ W, 1365 m.

*Umbellula spicata* Kükenthal

Indian Ocean

06° 24′ 01″ N, 49° 43·8′ E, east coast of Africa, 741 m. (Kükenthal 1902, type locality)
00° 27′ 04″ S, 42° 47·3′ E, 638 m. (*valdiviae* Kükenthal)
Andaman Is., 897 m. (*radiata* Thomson & Henderson)
03° 07′ 00″ S, 40° 45·8′ E, 748 m. (*valdiviae* Kükenthal)
09° 29′ 34″ N, 75° 38′ E, 659 m. (*elongata* Thomson & Henderson)
Andaman Is, 344–403 m. (*pendula* Thomson & Henderson)
13° N, 76° E, 1281–1098 m.

*Umbellula pellucida* Kükenthal

Indian Ocean

06° 24′ 01″ N, 49° 31·6′ E, 628 m. (Kükenthal 1902, type locality)
05° 15′ 48″–05° 13′ 42″ N, 73° 22′ 48″–73° 23′ 36″ E, 797 m. (*huxleyi* Hickson)
13° 16′ 00″–13° 16′ 36″ N, 46° 20′ 24″–46° 14′ 00″ E, 220 m. (*huxleyi* Hickson)
10° 48′ S, 123° 23′ E, near Rotti, 918 m.
13° 48′ 05″–13° 48′ 36″ N, 49° 16′ 48″–49° 16′ 24″ E, 2000 m. (*huxleyi* Hickson)
Andaman Is. (no other dates) (*purpurea* pars, Thomson & Henderson)

*Umbellula lindahli* Kölliker

Atlantic Ocean

71° 27′ N, 53° 58′ W, 223 m. and 70° 43′ N, 52° 03′ W, 752 m. (type localities of Lindahl's *miniacea* and *pallida*)
59° 29′ N, 07° 51′ W, 1061–1114 m.
52° 00′ N, 12° 06′ W, 846–934 m. (*ambigua* Stephens)
51° 58′ N, 12° 25′ W, 975–1007 m. (*ambigua* Stephens)
51° 36′ N, 11° 57′ W, 988–1208 m. (*ambigua* Stephens)
40° 33′–40° 34′ N, 35° 24′–35° 52′ W, 4600–4540 m. (*carpenteri* Broch)
Off Yucatan, 2869 m.
01° 03′–00° 58′ N, 18° 40′–18° 37′ W, 5250–5300 m. (*carpenteri* Broch)
64° 45′ N, 29° 06′ W, 1039 m.
61° 50′ N, 56° 21′ W, 2626 m.
Gulf of Gascogne 896 m. (*ambigua* Marion)
51° 59′ N, 12° 32′ W, 846–934 m. (*ambigua* Stephens)
51° 54′ N, 11° 57′ W, 641 m. (*ambigua* Stephens)
50° 42′ N, 11° 18′ W, 1148–1333 m. (*ambigua* Stephens)
38° 30′ 30″–38° 53′ N, 69° 08′ 25″–69° 24′ 40″ W, 3168–3720 m. (*Bairdii* Verrill)
Off Dominica, 2070 m.

Indian Ocean

01° 47′ 08″ S, 41° 58′ 08″ E, 1670 m. (*köllikeri* Kükenthal)
05° 40′ S, 132° 26′ E, near Kei Is., 310 m. (*antarctica* Hickson)
05° 40′ S, 120° 45′ E, near Saleyer, 1158 m. (*antarctica* Hickson)
07° 28′ S, 115° 24′ E, E. Bali Sea, 1060 m. (*antarctica* Hickson)
01° 57′ S, 73° 19·1′ E, 2919 m. (*rigida* Kükenthal)
05° 40′ S, 120° 45′ E, off South Celebes, 1158 m. (*Jordani* Hickson)
07° 28′ S, 115° 24′ E, near Bali, 1018 m. (*Weberi* Hickson)

Pacific Ocean

Off Kauai (near Hawaii) in four places, 705–2405 m. (*Jordani* and *Gilberti* Nutting)
32° 44′ 50″ N, 117° 48′ 45″ W, 448 m. (*magniflora* Nutting)
North-east point Santa Barbara I. N 89 W, 4·7 miles (California), 802 m. (*magniflora* Nutting)
46° 44′ N, 144° 02′ E, 928 m.
Shio Misaki Light N 49° E, 7 miles (Japan), 997–1303 m. (*magniflora* Nutting)
Near San Clemente I. (California), 604 m. (*loma* Nutting)
South-east point Santa Catalina I. 19° 30′ E, 3·2 miles (California), 611 m. (*magniflora* Nutting)
East point San Nicholas I. S, 7·6 miles (California), 395–620 m. (*magniflora* Nutting)
Off Omar Saki Light, Japan, 919 m.
34° 71′ N, 135° 39′ E, S. of Yeddo (Japan), 1034 m., bottom temp. 3·3° C. (*huxleyi* Kölliker)

Antarctic

46° 16′ S, 48° 97′ E (east of Kerguelen I.), 2938 m., bottom temp. 0·8° C. (*magniflora* Kölliker 1880, type)
70° 40′ S, 102° 15′ W, 2800 m.
Near Gauss-Berg, 2450 and 2725 m.
53° 55′ S, 108° 55′ E, 5310 m., and 62° 26′ S, 95° 44′ E, 3560 m. (type localities of *carpenteri* Kölliker 1880)
78° S, 174° E, 540 m.
East of Bouvet Is., 457 m. (*antarctica* Kükenthal, type locality)

Discovery localities

St. 180. 11. iii. 27. 1·7 miles W of N point of Gand I., Schollaert Channel, Palmer Archipelago, 160–330 m. (150 m., 0·00° C.).
St. 181. 12. iii. 27. Schollaert Channel, Palmer Archipelago, 64° 21′ 00″ S, 63° 01′ 00″ W, 335 m. (0·40° C.).
St. 182. 14. iii. 27. Schollaert Channel, Palmer Archipelago, 64° 21′ 00″ S, 62° 58′ 00″ W, 278 m. (0·12° C.).
St. 366. 6. iii. 30. 4 cables south of Cook I., South Sandwich Is., 77–152 m.
St. 371. 14. iii. 30. 1 mile east of Montagu I., South Sandwich Is., 90–161 m. (150 m. 0·44° C.).
St. 1644. 16. i. 36. 78° 24·8′ S, 164° 10·3′ W (Bay of Whales), 645 m. (585 m. ÷ 1·85° C.).
St. 1645. 17. i. 36. 77° 43·3′ S, 166° 18·2′ W, 475 m. (450 m. ÷ 1·85° C.).
St. 1652. 23. i. 36. 75° 56·2′ S, 178° 35·5′ W, 567 m. (541 m. ÷ 1·90° C.).
St. 1948. 4. i. 37. 60° 49·4′ S, 52° 40′ W, 490–610 m.

Although Pennatularians are rather scarce in oceanic collections, it is questionable whether the picture thus presented of their distribution and numerical occurrence on the sea-bottom is a true one. I have touched on this problem in a recent paper (Broch 1957). It is obvious that the catch depends to a great extent on the gear used, and unfortunately there is at present no gear able to catch more than a small percentage of all the specimens available. Mooring in the mud, flexibility, contractility, and strong holdfasts especially in the larger specimens, all combine to keep the Pennatularians anchored *in situ*. Some casual catches, nevertheless, show that some species at all events are patchy in occurrence. This is well known of shallow-water species like *Pennatula phosphorea*, *Virgularia* and *Stylatula* among others, and latterly it has been observed in some species of *Umbellula*; for example, about 240 specimens of *U. pellucida* were taken at St. 194 by the 'John Murray' Expedition (Hickson 1937), 45 *U. thomsonii* at Discovery Station 342, and 157 specimens at St. 362 by the Swedish Deep-Sea Expedition.

In this connexion, it should be noted that bottom samplers (grabs) do not catch Pennatularians even at localities where other gear proves them to be comparatively numerous. It is most probable that the *larger*, slender, very flexible, deeper-living sea-pens cannot be caught by the grabs, which therefore only give a fragmentary picture of the momentary balance in populations of the *medium-sized* bottom animals.

In spite of these negative results, however, a review of the many scattered localities (text-fig. 4) gives us a few hints as to the environmental requirements of *Umbellula* and the distribution of the species.

*U. durissima* has only been captured singly at depths from 1012 to 4474 m. The stem is very flexible, and most specimens evidently escape the usual fishing gear. Curiously enough one of the first specimens was captured in antarctic waters, where the species has never since been observed. All other records are from intermediate depths in the tropical and subtropical regions of the Atlantic, Indian and Pacific Oceans.

*U. thomsonii* appears to be plentiful in the deeper waters of the Atlantic and Indian Oceans (from 1336 down to 5860 m., mostly below 3000 m.), but from Pacific waters only two young specimens have been recorded from 3750 and 4460 m. The largest catches to date were made by the Swedish Deep-Sea Expedition in the Atlantic Ocean, where at St. 342 (5033 m.) the prawn otter-trawl caught 45 specimens, and at St. 363 (5300 m.) 157 specimens. The species appears to avoid territories where arctic or antarctic waters influence the bottom conditions, although low temperatures may not necessarily be the main factor.

*U. huxleyi* has been found in a few, very scattered places in the Atlantic, Indian and Pacific Oceans, generally in tropical and subtropical areas at depths between 296 and 1365 m. The widely spread localities and the records only of single specimens were even more conspicuous than in *U. durissima*, until the remarkable catch made by Dr A. R. Longhurst in 1955 off Bissago I. (Port Guiana), where one haul of the otter-trawl yielded no less than 17 specimens at 600 m. depth. Not only had a 'patch' been found, but by good fortune the gear also chanced to detach all these specimens from the mud. (Whether this was just a stroke of luck in sampling the elusive benthos is another question.) The catch may indicate that optimum conditions existed here at about 600 m. depth, though on comparison with other records, with one exception situated at greater depths and at lower temperatures, this appears very remarkable.

Only two very characteristic *Umbellula* species have so far been located in the Indian Ocean alone. Several 'species' have been described from the Indo-Malayan region, but most of them must be reduced to synonyms. Hickson (1937) touched on the problem in his own way saying: 'It is very improbable that a larger number of specimens belonging to the same genus, and all in approximately

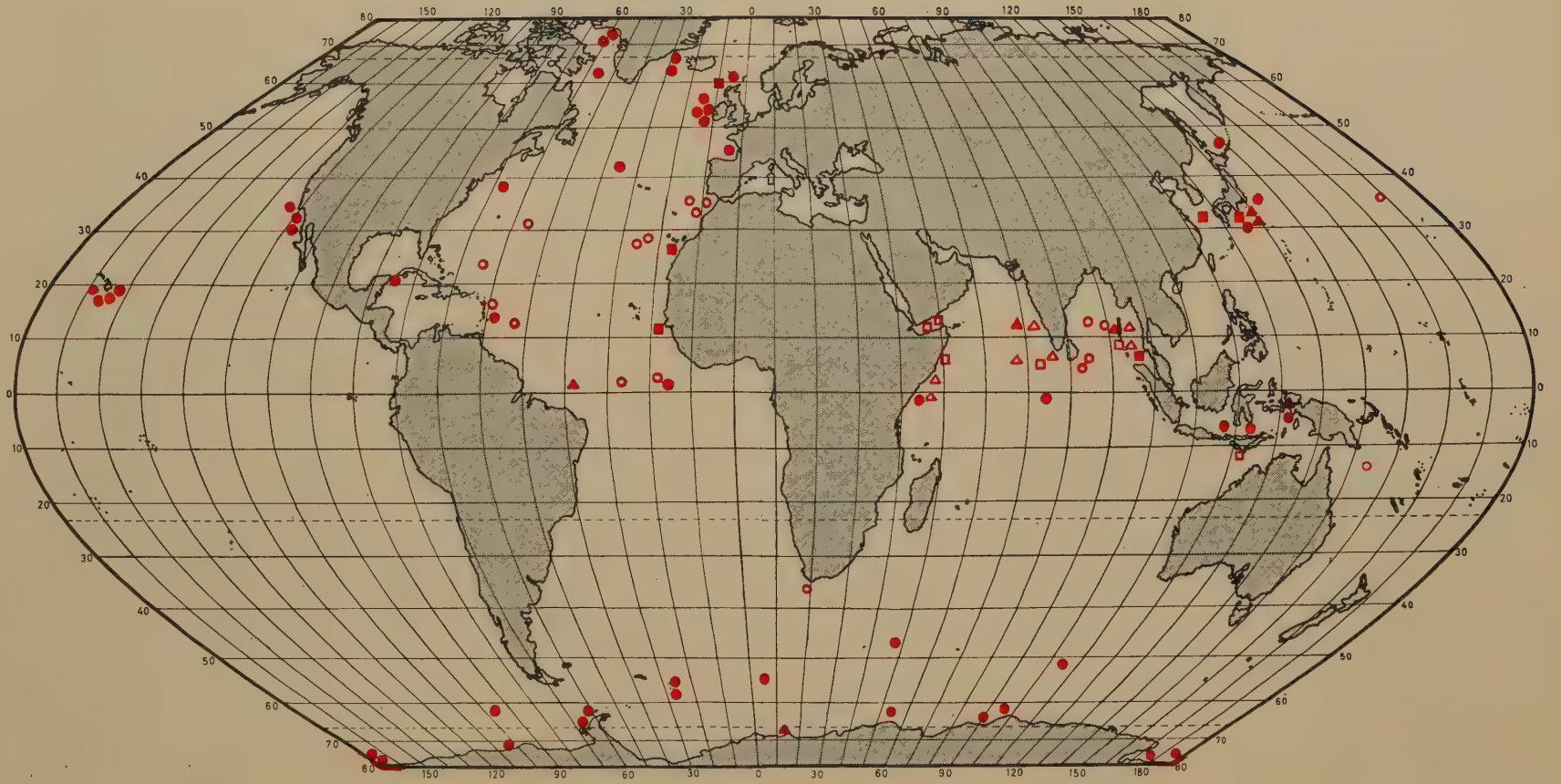

Fig. 4. Records of *Umbellula* (North Polar Sea with *U. encrinus* excluded: see fig. 5). *U. durissima* ▲; *U. thomsonii* ○; *U. huxleyi* ■; *U. spicata* △; *U. pellucida* □; *U. lindahli* ●.

the same sexual condition, living in the same locality in deep water, should belong to more than one species. Any cross-fertilization that might occur would soon swamp any specific distinctions.' This of course to a great extent depends on what we consider as specific characters. Nearly related species may according to the laws of heredity live and propagate side by side and nevertheless keep their specific identities intact, and so far as we know this is as true for the deep sea as for every other domain. The Indian Ocean contains an extraordinarily rich fauna in its deeper regions, but at present we do not know, which factors, or combination of factors, make this ocean especially favourable for *Umbellula* and for the moment it must suffice to record the known facts.

*U. spicata* appears to be confined to the Indian Ocean and at the same time has a remarkably narrow bathymetrical range between 344 and 1281 m. Different growth stages have been interpreted as distinct species, and because of the great flexibility of the stem, adult specimens had not been caught and described hitherto.

*U. pellucida* also seems to be restricted to the Indian Ocean. Its known bathymetric range is from 220 to 2001 m. It is noteworthy that the deepest haul only gave one specimen, whereas the haul in 220 m. resulted in some 240 specimens; also one haul in 625 m. depth gave 8 specimens, all other catches consist of 1 or 2 specimens. This may be taken as an indication that the upper part of the habitat offers the optimum conditions, and that the deepest locality, separated widely from the next record, shows an erratic individual which has grown up below the normal habitat of the species.

*U. lindahli* is the most widespread species of the genus, and if *U. encrinus* turns out to be an ecologically distinct form, the species inhabits all oceans. At the same time the bathymetric range—77–5310 m.—is much greater than in the other species. Most of the earlier records in the Antarctic region were from great depths, from 2450 to 5310 m., and only two localities showed depths as shallow as 540 and 457 m. It was therefore surprising that all the nine Discovery Stations lie between 645 and 77 m.

It has been rather usual to regard temperature as the deciding factor, when deeper living bottom animals ascend in higher latitudes to lesser depths than elsewhere. *U. lindahli*, on the other hand, is remarkable in that both the deepest locality (5310 m.), and the shallowest (77 m.) are situated in Antarctica, and that the deepest record here almost coincides with depths in the Atlantic near the equator.

One may say that generally the more robust and better developed specimens have been observed in Antarctica, the slenderer specimens in deeper waters of the tropical seas. However, there are exceptions, e.g. the comparatively short and fleshy '*antarctica*' specimens are common both in the Antarctic and in the tropical part of the Indian Ocean. The question of geographically distinct varieties in *U. lindahli* must also be considered.

In spite of comparatively numerous localities (cf. text-fig. 4, 49 records, 16 of which are in Antarctic waters) the evidence is scanty, and it is not astonishing that *U. lindahli* has been described under several names, which in some cases might seem to indicate local races. The Discovery collections have proved that the three 'species' only described from Antarctic waters represent either developmental phases, or more or less luxuriant individuals. '*U. carpenteri*' doubtless represents younger stages in most cases and larger specimens cannot be distinguished from '*U. magniflora* (*ambigua*)'. Nothing indicates that these forms are restricted to special geographical areas. A more luxuriant development of the cluster leads from *U. magniflora* to *U. antarctica*; from the specific name one might assume that the latter represented a special Antarctic variety, but typical *U. antarctica* are also comparatively frequent in tropical Indian waters.

The accessible data do not yet indicate geographical races, or varieties, in *U. lindahli*. On the

contrary, we can say that the more extensive our material has become, the more indefinite are the limits which earlier seemed to point in the direction of local 'species'.

Nevertheless, we must make one reservation as to the high-arctic *U. encrinus* already mentioned on page 270. A study of its occurrence (text-fig. 5) indicates that it must have penetrated into the Polar deep and into the cold bottom water of the Davis Strait and Baffin Bay from the Atlantic Ocean. In the Polar Sea it has been found in water as shallow as 180 m., and it is therefore astonishing that the species apparently has not been able to pass beyond the submarine Lomonosov mountain range into the western part of the Polar Basin.

Geographical distribution seems to indicate that *U. encrinus* in reality is an ecologically distinct group. It must have invaded its two distinct habitats from the more temperate Atlantic bottom waters. The western habitat in Davis Strait and Baffin Bay is barred to the north by shallow thresholds from the central (both eastern and western) Polar Deep, and communication with the eastern north Atlantic–Arctic deep sea, north of the Scotland–Iceland–Greenland ridges, round the southern part of Greenland seems unlikely in the present state of our knowledge. It is, therefore, natural to assume that penetration was originally via the Atlantic bottom water into the Davis Strait, and that a secondary invasion occurred over the submarine ridge in the Faroe Channel. This double origin in Arctic waters of *U. encrinus* favours considering it as an ecologically distinct, geographical variety, and not as a genetically separate species.

A study of Jungersen's (1916, 1919) papers indicates that the morphological differences between *U. lindahli* and *U. encrinus* are more fluid in the Davis Strait, where no prominent submarine ridges accentuate the biophysical border lines as do the submarine ridges from Scotland past the Faroes and Iceland to East Greenland. But in spite of this the gap between the Arctic and the Atlantic groups is so conspicuous that at present it is more convenient to treat *U. lindahli* and *U. encrinus* as separate species.

It is striking that *U. encrinus* is much more coarse and luxuriant than the largest Antarctic specimens of *U. lindahli* hitherto captured. If the first is an extreme geographical race, the question again arises, why the Antarctic specimens do not attain such large dimensions as the Arctic. Are conditions of life subjected to greater fluctuations and, therefore, less favourable in Antarctic waters, than in the much more sharply circumscribed Arctic deep sea?

## PENNATULIDAE

### *Pennatula rubra* Ellis 1764

(Synonymy before 1910, see Kükenthal and Broch 1911)

*P. rubra* Kükenthal & Broch 1911, p. 382, text-figs. 182–7.

*P. rubra* Kükenthal 1915, p. 91, figs. 98, 99.

*P. rubra* Hickson 1916, p. 183.

St. 272. Off Elephant Bay, Angola, 200–230 m. 9 specimens (three of them identified by Mrs MacFadyen) from 13 to 25 cm. length.

St. 2633. 13° 11·5′ S, 12° 44·1′ E (off mouth of Elephant Bay, Angola) 104–? (sounding 91–104 m., but a note states that the net was fishing clear of the bottom at the end of the haul). 1 specimen, length 11 cm.

The specimens from St. 272 vary much in length, and so does the length of the stalk, which generally measures one-half to one-quarter of the entire specimen. It is of interest to note that the larger specimens are much more inflated than the smaller ones, which are rather contracted, although not so strongly as the specimen from St. 2633, which has a total length of 11 cm. only. Evidently the length of the specimen depends to a certain degree on the degree of contraction, and a living *Pennatula rubra* doubtless shows a great faculty of inflation by imbibing water. This influences the colours also. The

Fig. 5. The distribution of *Umbellula encrinus* in the North Polar Sea (after Broch, 1956). The submarine Lomonosov Ridge from Greenland to the New Siberian Islands is indicated.

spicules generally are dark, almost blood red, and the more inflated the specimen is, the more pinkish it becomes, whereas strongly contracted specimens like that from St. 2633 are dark red, especially on its leaves and rachis. In such specimens, however, the longitudinal dorsal white band along the rachis is extraordinarily obvious and comparatively broad. In the specimen from St. 2633 the 5 cm. long stalk is yellowish white.

At a first glance this strongly contracted specimen recalls *P. phosphorea* f. *variegata*. Earlier authors like Kükenthal and Broch (1911) have generally emphasized the spongy tissues of *P. rubra*, which enables it to extend markedly, but nobody seems on the other hand to have hinted at its strikingly great faculty of contraction. This power is comparable with that of *Pteroëides griseum* (comp. Niedermayer 1911). In *Pennatula* the colour is confined to the spicules, and the shade of the colour of a specimen will therefore depend to a great extent upon its state of dilation or contraction. This was easily seen in the 10 specimens from the Discovery collections, the specimens of which were very differently expanded.

*P. rubra* is characterized in the literature as a Mediterranean species. Looking at the few localities which are sufficiently precise to plot on a chart (fig. 1, p. 249), the species, like *Cavernularia elegans*, (p. 250) seems to belong zoogeographically to the same group as *Veretillum cynomorium*; more localities are recorded from the Atlantic Ocean than from the Mediterranean. Like *V. cynomorium* also, *Pennatula rubra* seems to have its eastern border in the Mediterranean off southern Italy; along the eastern coasts of the Atlantic, it is distributed from Portugal and southwards to Angola, and its bathymetric range lies between 60 and 230 m. depth.

## PTEROËIDIDAE

### *Pteroëides griseum* (Bohadsch 1761)

(Synonymy before 1910, see Kükenthal and Broch, 1911)

*P. griseum* Kükenthal 1915, p. 98, figs. 104–7.
*P. griseum* Hickson 1916, pp. 219 et seq.
*P. spinosum* Pax & Müller 1953, p. 31.
*P. griseum* Broch 1953, p. 15.
*P. spinosum* Pax 1956, p. 59.
St. 2634, 12° 17·4′ S, 13° 31·3′ E, 80–91 m. 1 specimen, total length 20 cm.

The specimen is rather strongly contracted, although its total length is 20 cm. However, the total length (or height) of a specimen of *Pteroëides* is rather problematical, because of its enormous faculty of inflation and contraction. This is easily observed in aquaria. By night I have observed specimens of *P. griseum*, the raches of which have expanded to about 1 ft. in height above the mud with a breadth of 4–5 in., whereas by day the same specimens had contracted to a length of 4–5 in., only a couple of inches broad, and all but entirely buried in the muddy bottom; in this case the leaves were moreover packed against each other along the stem.

Most authors have admitted two varieties of *P. griseum*, var. *longispinosum* and var. *brevispinosum* (see Kükenthal 1915, p. 99). The Discovery specimen is of special interest in this connexion. Most of its leaves belong to the *brevispinosum* type, but some of them are decidedly of the *longispinosum* type. This supports Kükenthal's (1915) words, that the two varieties instituted by Kölliker 'nicht scharf getrennt sind'.

Hickson (1916) was of the opinion that the numbers of rays in the leaves in the middle of the rachis must be looked upon as the most important specific character. This character, however, is only of mediocre value, being useful only in adult specimens. Thus Hickson placed *P. lusitanicum* Broch in

a different group of the genus to *P. griseum*, whereas the first-named species is based most probably on a young specimen of the latter. To solve this question very extensive material is necessary.

According to the literature, *P. griseum* seems to be comparatively common in the Mediterranean, at all events as far east as the Adriatic. In the Atlantic Ocean it has been reported from the European coasts as far northwards as the Faroes (Kükenthal 1915), but up till now it does not seem to have been reported from the coast of Africa. The species lives in tolerably shallow water, but when we consider its biotope with the soft muddy bottom, and its mode of life in daylight almost entirely burrowed in the mud, it is easily understood that it had hitherto escaped the investigators. The Discovery record seems to indicate that *P. griseum* almost coincides zoogeographically with *Cavernularia elegans*, *Veretillum cynomorium* and *Pennatula rubra*.

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* Quoted from Pax and Müller 1954.

# PLATE XI

Fig. 1. *Umbellula huxleyi* Kölliker. Two specimens from off Bissagos I. (Port Guiana), 600 m. (natural size). (*a*) the smaller specimen, autozooids not ripe, devoid of eggs; (*b*) the larger specimen, autozooids filled with eggs.

Fig. 2. *Umbellula spicata* Kükenthal. The polyp tassel of the specimen from 13° N, 76° E, 600–700 fthms (natural size). The basal parts of the autozooids are crammed with eggs.

Fig. 3. *Umbellula carpenteri* Kölliker 1880, specimen A. Cluster in ventral view (× 2). The budding fifth autozooid is distinctly seen in the middle below the acute top of the rachis. The specimen is a juvenile stage of *Umbellula lindahlia*.

1a
2
1b
3

# PLATE XII

Fig. 4. *Umbellula pellucida* Kükenthal. Two specimens from the John Murray Expedition Station 194. The stalk is rigid and straight, but has been artificially coiled when photographed; it is easily seen in the figures that the axis was thereby fractured in some places (natural size). *a*, an unripe specimen without eggs in the autozooids. *b*, a ripe specimen with autozooids crammed with eggs.

Fig. 5. *Umbellula lindahli* Kölliker. Cluster of a typical *magniflora* specimen from 'Discovery' St. 366, No. 4 of the table (natural size).

Fig. 6. *Umbellula lindahli* Kölliker. Tassel of an *antarctica* specimen from 'Discovery' St. 366, No. 1 of the table (natural size).

4a
4b
5
6